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Research Article

Soil macroarthropod communities of Amazon degraded pastures restore differently during their natural regrowth

Daniel Castro[1], Clara P. Peña-Venegas[1], Carlos H. Rodríguez-León[2,3], Ervin H. Duran-Bautista[4,5], Armando Sterling[3]

1 *Laboratorio de Microbiología y Biología de Suelos, Instituto Amazónico de Investigaciones Científicas SINCHI, Leticia, Amazonas, Colombia*
2 *Programa Modelos de Funcionamiento y Sostenibilidad, Instituto Amazónico de Investigaciones Científicas SINCHI, Florencia, Caquetá, Colombia*
3 *Laboratorio de Fitopatología, Instituto Amazónico de Investigaciones Científicas SINCHI – Facultad de Ciencias Básicas, Universidad de la Amazonía, Florencia, Caquetá, Colombia*
4 *Programa de Ingeniería Agroecológica, Universidad de la Amazonia, Florencia, Caquetá, Colombia*
5 *Laboratorio de Ecología del Suelo, Grupo de Investigación en Agroecosistemas y Conservación en Bosques Amazónicos– GAIA, Florencia, Colombia*
Corresponding author: Daniel Castro (jcastro@sinchi.org.co)

Abstract

Understanding the recovery of soil macroarthropod communities during natural regrowth is crucial to demonstrate complete soil restoration. This is because these organisms can play a key role in shaping soil structure and community dynamics, making them essential to understanding these processes. This study investigates the recovery of soil macroarthropod diversity, density, and biomass across different stages of natural regrowth, focusing on the taxonomic groups and feeding guilds dynamics. Macroarthropod communities were analyzed along a chronosequence (young-age, middle-age, and old-growth) including their vertical distribution (litter, 0–10 cm, 10–20 cm, and 20–30 cm). A total of 20 plots and 100 Tropical Soil Biology and Fertility Programme (TSBF) soil monoliths were sampled. Results revealed an increase in total macroarthropod diversity, biomass, and density with regrowth, but these patterns do not occur in the same way for all macroarthropod groups, emphasizing the complexity of ecological succession. Termites were key ecosystem engineers, shaping community composition at each regrowth stage. Predators and decomposers also exhibited significant changes in response to regrowth, reflecting their sensitivity to ecological disturbances. In contrast, ants and some herbivores showed higher densities and biomass in pastures and early regrowth stages, with notable shifts in species composition over time. Vertical distribution of macroarthropods revealed higher activity at the 0–10 cm depth, with similarities in the composition in litter and 10–20 cm soil depth, highlighting soil microarthropod importance in soil mineralization and humification. These findings underscore the critical role of ecosystem engineers in soil restoration and highlight the need for the conservation of soil biology to enhance soil health.

Key words: Density, diversity, ecosystem engineers, feeding guilds, macroarthropod mass, natural restoration

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Introduction

Soil is probably one of the most complex and species-rich habitats of the world (FAO et al. 2020). Soils host up to 59% of the world's living species, which are associated with the soil at some stage of their life cycle (Decaëns et al. 2006; Orgiazzi et al. 2016; Anthony et al. 2023). Soil macrofauna is an important reservoir of global biodiversity and may constitute a large part of the total soil faunal biomass (Gongalsky 2021; Lavelle et al. 2022), with an important role in ecosystem functions (Guerra et al. 2020). Soil macrofauna participate directly and indirectly in most key soil functions such as organic matter decomposition, nutrient cycling, energy flow, carbon storage, soil water regulation, among others (Brussaard et al. 2007; Lavelle et al. 2022). Among soil macrofauna, certain groups, such as earthworms and social insects like termites and ants, act as ecosystem engineers by significantly modifying soil structure and processes (Sanders and van Veen 2011; Bottinelli et al. 2015; Phillips et al. 2021). Among them, soil macroarthropods, capable of modifying soil profiles, play a crucial role in tropical soils where they strongly influence organic matter cycling processes. Macroarthropods also fragment a large portion of the available soil necromass and are responsible for predating a significant portion of edaphic communities (Lavelle et al. 1994; Andriuzzi and Wall 2018; Griffiths et al. 2019). Soil macroarthropods, especially social insects such as termites and ants, represent a significant portion of soil biomass in tropical ecosystems (Fittkau and Klinge 1973; Barros et al. 2002), with a high number of species and functional groups (Brussaard et al. 1997; Gerlach et al. 2013; Paquin and Coderre 2017; Forstall-Sosa et al. 2021). However, soil macrofauna is one of the most underestimated components of tropical ecosystems (Gongalsky 2021; Mathieu et al. 2022).

Deforestation is one of the main threats for soil diversity as it ushers in drastic changes in vegetation, soil composition and soil structure (Franco et al. 2019; Veldkamp et al. 2020). However, habitat fragmentation—often associated with deforestation and the expansion of agricultural frontiers—represents another critical threat to biodiversity in tropical soils. Fragmentation alters abiotic conditions, affects soil biotic interactions, and leads to time-delayed biodiversity losses across multiple trophic levels (Krauss et al. 2010). In the Neotropical region, these processes are strongly linked to a decline in species populations and the disruption of ecosystem functions (Liu et al. 2018). Despite its profound effects, fragmentation remains an underexplored factor in studies on soil macrofauna in the Amazon region.

The FAO FRA 2020 report indicated that between 2000 and 2018 the highest rates of world deforestation occurred almost entirely in South America (FAO 2021), one of the less studied areas in soil biodiversity (Cameron et al. 2018; Guerra et al. 2020). In South America, the highest rates of deforestation occurred in the Amazon basin (Aide et al. 2013; Pendrill and Persson 2017; Kalaiyarasi et al. 2023), where livestock farming, mining, agriculture and oil exploitation are the main activities associated to it (Armenteras et al. 2013; González-González et al. 2021; Lapola et al. 2023). Deforestation affects directly biotic and abiotic components of soil, threatening essential soil functions and the biodiversity that supports ecosystem resilience in tropical regions (Veldkamp et al. 2020; Qu et al. 2024).

Deforestation in Amazon ecosystems usually reduced abundance, biomass and species richness of soil macroarthropods (Marichal et al. 2014; Franco et al. 2019; Serra et al. 2021), and it is directly related to the magnitude of the perturbation; it

also impacts the taxonomic composition and functional structure of soil macroarthropods (Barros et al. 2004; Borges et al. 2021; Pollierer et al. 2021). Additionally, deforestation affects the abundance and richness of predators more than those of other soil macroarthropod communities (Rousseau et al. 2014). Converting forest to pastures, reduces soil macrofauna taxa up to 70% (Franco et al. 2019).

A better understanding of how soil communities respond to deforestation and habitat fragmentation, and how it is restored is crucial to enhance policies that effectively protect soil biodiversity, soil ecosystem services and guarantee the restoration of all the components of the ecosystem (Franco et al. 2019). Diverse active and passive restoration strategies have been implemented in the Amazon region to restore the ecosystem (Uhl et al. 1988; Schroth et al. 2015; Guerra et al. 2020; Vieira et al. 2021), but few of them included the study of biological communities, with soil macroinvertebrates, excluding earthworms, being especially neglected. Soil macroinvertebrate communities play a pivotal role in soil recovery, reflecting the gradual process of soil rehabilitation through their functional and taxonomic composition (Barros et al. 2004; Meloni and Varanda 2015; Cole et al. 2016; Serra et al. 2021).

Soil macroarthropod groups respond differently to soil changes (Suárez et al. 2018; Tulande-M et al. 2018; Vazquez et al. 2020; Rodríguez-León et al. 2021; Duran-Bautista et al. 2023). Studies in the Amazon region indicated that soil macroarthropod recuperates after 7 years of an active or passive restoration, with density and diversity values similar to those found in an old secondary forest, (Benito et al. 2004; Guimarães et al. 2020). However, there is scant evidence as to whether soil macroarthropod community composition is similar to that found in a primary Amazon forest and whether its vertical distribution and feeding guilds composition are recovered over time. It has been evidenced that the greatest dynamics of soil macroarthropods occur within the top 15 cm of soil (Amazonas et al. 2018), but many organisms are known to inhabit depths of up to 30 cm (Araújo et al. 2010). This underscores the need for further exploration of these dynamics, particularly in the context of soil regeneration processes.

This work aims to contribute to understanding temporal changes in diversity and feeding guilds composition on soil macroarthropod communities and functional restoration of Amazon soils in a chronosequence of degraded pastures undergoing natural regeneration through its natural regrowth. We hypothesize that natural regeneration promotes the progressive recovery of soil macroarthropod diversity, mass, and guild composition, ultimately resembling the communities and functions of undisturbed forests. Specifically, we predict that soil macroarthropod diversity and density will increase over time, driven by improvements in soil physicochemical properties, and that older regrowth stages will converge in community composition and guild structure with those observed in primary forests.

Materials and methods

Site description

The study area was located in the northwestern Colombian Amazon, in the rural areas of the municipalities of Belén de los Andaquíes (1°24'59.1"N, 75°52'21.2"W), Florencia (1°36'50"N, 75°36'46"W), Morelia (1°29'09"N,

75°43'28"W), and San José del Fragua (1°19'52"N, 75°58'28"W), in Caquetá state (Fig. 1). Sampling took place during the dry season, from December 2018 to February 2019. The study area, characterized by an average altitude of 416 m, receives an annual precipitation of 3235 mm and has an average temperature of 25.1 °C (Murad and Pearse 2018). The soils in the study area, classified as Oxisols and Ultisols (USDA), exhibit low pH (4.5–5.8), high clay content with kaolinite and quartz, drainage limitations, aluminum saturation, and low levels of carbon, potassium, phosphorus, and magnesium in the mineral horizons (IGAC 2014).

A total of 20 sites were sampled using a stratified random probabilistic sampling approach, classified into four distinct natural regrowth ages: (i) pastures with approximately 10 years of use for livestock farming, characterized by degraded *Brachiaria* spp.; (ii) young age fallows (between one to 10 years old), with shrubby vegetation dominated by species from the Melastomataceae, Mimosaceae, and Rubiaceae families, and a gradual increase in species density, with *Miconia elata*, *Miconia minutiflora* and *Miconia lourtegiana* being the most abundant species; (iii) middle-age fallows (between 11 to 20 years old) with pioneer tree species from the Fabaceae and Mimosaceae families, and common species such as *Siparuna guianensiss*, *Henriettea fascicularis*, *Adenocalymma aspericarpum*, *Piptocoma discolor* and *Inga thibaudiana*; and (iv) old-growth fallows (between 21 to 30 years old), similar to intermediate secondary forests dominated by pioneer trees such as *Tapirira guianensis* and *Adenocalymma aspericarpum*, with a more complex forest structure and higher species diversity, particularly from the Rubiaceae, Mimosaceae, Moraceae, Fabaceae, Annonaceae and Lauraceae families. From each regrowth stage, five plots of 60 × 60 m (0.36 ha) were sampled, resulting in a total of 100 plots when considering all regrowth stages combined (Suppl. material 1).

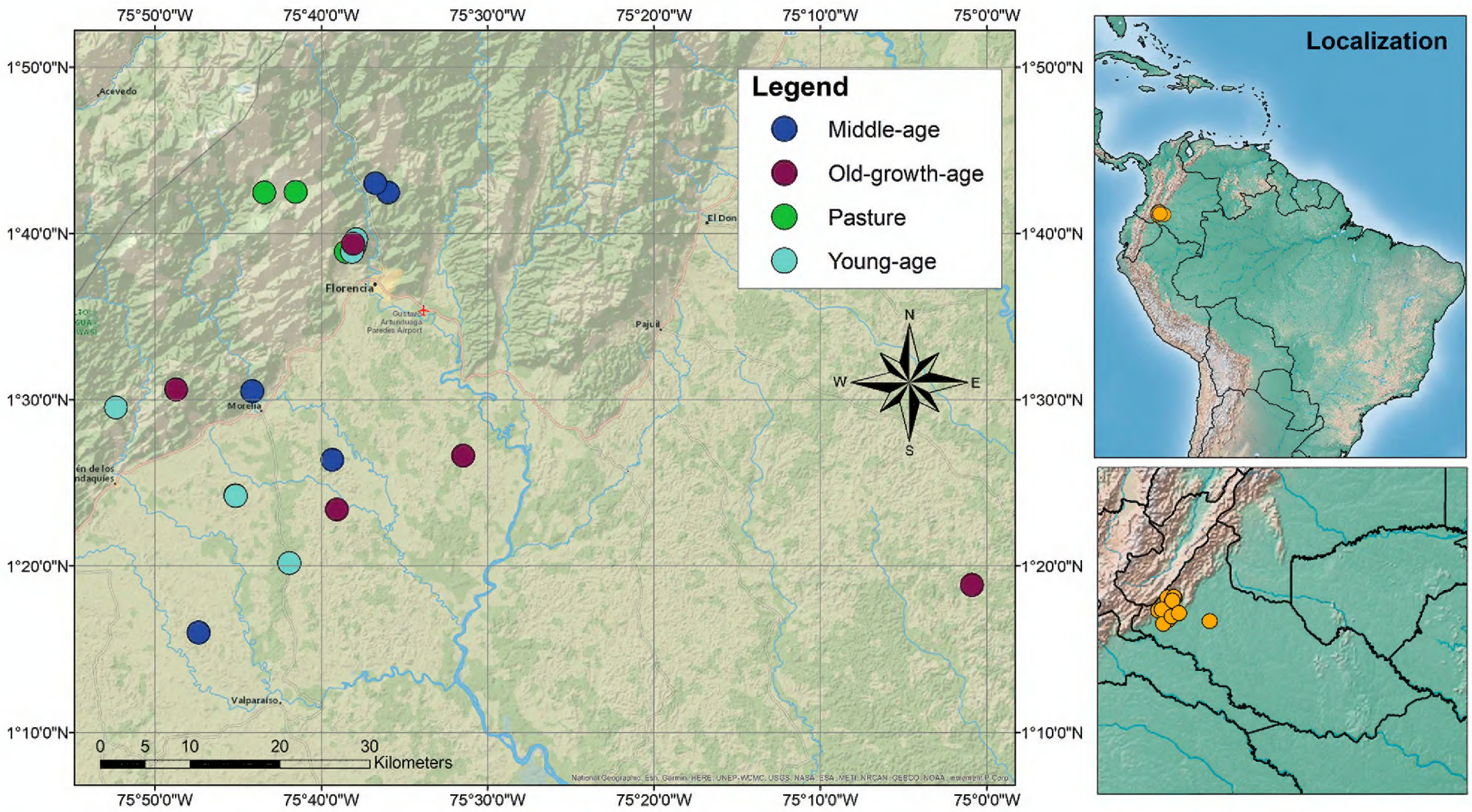

Figure 1. Localization of the study sites in the Northwestern Colombian Amazon.

Soil macroarthropod sampling collection

The Tropical Soil Biology and Fertility Program (TSBF) (Anderson and Ingram 1993, ISO 2011) sampling method based on the collection of soil monolith was used. Within each sampling site, a 60 × 60 m plot was delimited. Within each plot, five points were located to obtain a 25 × 25 × 30 cm monolith at each point, resulting in a total of five monoliths per plot, 25 monoliths per regrowth age and 100 monoliths in total. Each monolith was divided into four depths: litter, 0 to 10 cm, 10 to 20 cm, and 20 to 30 cm. Soil volumes from each depth were extracted using paddles and examined manually in the field with tweezers and brushes to capture all arthropods present. Arthropods were preserved in 96% ethanol and labeled for subsequent cleaning and taxonomic identification at the laboratories of the SINCHI Institute. Additionally, a composite soil sample of 500 g from the 0–15 cm soil depth was taken from each plot for physicochemical analysis.

Soil macroarthropod identification and feeding guilds

Earthworms and mesoarthropods such as Collembola and Acari were not included, focusing our analysis on macroarthropod communities instead. All macroarthropod individuals were identified and morphotyped according to their morphology (Ruiz et al. 2008). Specimens were identified at family or order level (Borrow et al. 2000; Adis 2002; Casari et al. 2024), but termites and ants were identified to the genus or species level (Krishna and Araujo 1968; Constantino 2002; Rocha and Cancello 2007, 2022; Acioli and Constantino 2015; Castro and Scheffrahn 2019; Fernández et al. 2019; Carrijo et al. 2020, 2023). Four feeding guilds were established based on the feeding habits and roles in the ecosystem: decomposers (or detritivores), predators, herbivores (or phytophages), and omnivores (Brussaard 1998; Brandão et al. 2012; Lamarre et al. 2016, de Souza and Freitas 2018). The assignment of these groups to the macroarthropod morphotypes was done at a higher resolution for some taxonomic groups as there are differences in diet within certain taxonomic groups or there is limited biological knowledge about it. Thus, according to bibliography and field observations for Diplura, Japygoidea was classified as predators, while other morphotypes were classified as decomposers (Reddell 1983). For Opiliones, the suborder Laniatores was categorized as predators, and other morphotypes as decomposers (Acosta and Machado 2007). The complete classification for each morphotype is provided in Suppl. material 2.

Macroarthropod density (individuals/m^2) was estimated by counting the number of individuals within the monolith area. Drying the samples is a destructive method, and given the value these specimens hold for the region, we decided not to dry them. Instead, an approximation of biomass was obtained through the mass in alcohol from individuals preserved in ethanol by placing them on filter paper to remove the excess of liquid and then weighing them on a precision scale with an accuracy of 0.0001 g. Mass in alcohol was interpreted in two ways: in grams per square meter (gr/m^2) and in milligrams per square meter (mg/m^2). Raw data on density and mass in alcohol for each morphotype are also described in Suppl. material 2.

All specimens were deposited in the “Colección de artrópodos terrestres de la Amazonia Colombiana – CATAC” of the Sinchi Institute, located in Leticia, Amazonas, Colombia.

Soil physicochemical analysis

Nineteen soil parameters were evaluated: pH (1:1 in water); electric conductivity (EC) with a saturated soil paste (Corwin and Yemoto 2017); cation exchange capacity (CEC), base cations (calcium, potassium, and sodium) using ammonium acetate extraction at soil pH = 7; bulk density (BD) from a cylinder volume; Organic carbon (OC), and total nitrogen (N) by Walkley-Black method (Walkley and Black 1934); soil texture (Clay, Silt and Sand percentage) using Bouyoucos method (Bouyoucos 1936); iron (Fe), copper (Cu), and Zinc (Zn) with acid Mehlich solution; phosphorus (P) and boron (B) using colorimetric method. Additionally, the O and A horizons were measured directly in the field in a 15 cm depth profile. Soil samples for physicochemical analysis were analyzed in AGRILAB laboratories using standardized protocols certified by ONAC-Colombia.

Data analysis

Macroarthropod alpha diversity was evaluated through rarefaction and extrapolation curves, calculated from the species accumulation data. These curves were generated using the R package "iNEXT" (Chao and Chiu 2016; Hsieh et al. 2016), with extrapolation from the observed 25 monoliths to 40 monoliths to account for potential under-sampling. Rarefaction curves were computed with 100 bootstrap replications to generate 95% confidence intervals, allowing for robust comparisons of diversity between regrowth ages.

Generalized Linear Mixed Models (GLMMs) were employed to analyze the dependent variables: soil macroarthropod density, mass, and species richness, as well as their vertical distribution across soil layers. Given the overdispersed nature of count data for density and richness, as well as the skewed distribution of biomass data, negative binomial and Poisson distributions were utilized, respectively. The GLMMs were fitted using the "lme4" package (Bates et al. 2021). In these models, regrowth age (as part of the chronosequence) was treated as a fixed effect because it represents a predictor of primary interest, directly hypothesized to influence macroarthropod abundance, biomass, and richness. Similarly, for the vertical distribution analysis, depth (litter, 0–10 cm, 10–20 cm, and 20–30 cm) was included as an additional fixed effect, as it represents another factor hypothesized to affect the distribution of macroarthropods. We also included the interaction term between regrowth age and depth to assess how the effect of regrowth age varies across soil layers. Plot and monolith were modeled as random intercept effects to account for spatial variability and the nested sampling structure. Monoliths, representing independent sub-samples within each plot, were considered the true replicates in this analysis. Predictions from the final GLMMs were visualized using the "sjPlot" package (Lüdecke 2024), with the predicted marginal means and 95% confidence intervals plotted for species richness, density, and biomass (mass in alcohol) for the taxonomic groups showing the highest variance, as identified by the GLMM results, across different regrowth ages.

The soil physicochemical variables were also analyzed using GLMMs, employing similar Poisson or negative binomial distributions based on the AIC for model selection. The relationship between physicochemical variables and macroarthropod metrics (density, biomass, and richness) was evaluated by adding the relevant soil variables as fixed effects in the models.

Model selection was based on evaluating the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC), ensuring the parsimony and fit of the models. Overdispersion was evaluated by comparing the residual deviance to the degrees of freedom, and in cases of overdispersion, negative binomial models were preferred over Poisson models. The final models were chosen based on AIC and residual diagnostics. In cases where multiple models had similar AIC values ($\Delta AIC < 2$), the simplest model (i.e., with fewer parameters) was selected following the principle of parsimony.

Post-hoc comparisons of fixed effects were performed using Fisher's Least Significant Difference (LSD) test, with a significance level of 0.01. These comparisons were implemented via the "multcomp" package (Hothorn et al. 2008, 2023), adjusting for multiple comparisons when necessary. To interpret the effect sizes, standardized regression coefficients were reported alongside 95% confidence intervals.

To assess patterns in the taxonomic composition of macroarthropods and their relationship with soil physicochemical properties, a Principal Component Analysis (PCA) was conducted. The PCA was performed using the "factoextra" (Kassambara and Mundt 2020) and "FactoMineR" (Lê et al. 2008; Husson et al. 2020) packages. The PCA incorporated regrowth age, the most significant soil physicochemical variables (as indicated by GLMM results), and taxonomic groups with notable variations across stages of succession, the four feeding guilds, and the ecosystem engineers as an additional group (termites and ants). Before conducting PCA, all continuous variables were scaled to have zero mean and unit variance to ensure comparability. To evaluate the statistical significance of the principal components and the overall ordination, a Monte Carlo permutation test with 999 permutations was applied using the "ade4" package (Dray et al. 2020). This test allowed us to assess whether the observed patterns were significantly different from those expected by chance.

Pearson correlation coefficients were calculated for each variable in relation to the principal components, and their statistical significance was determined to identify the variables contributing most to the observed variation in community structure and physicochemical properties. The results of the PCA were visualized using biplots, with vectors representing the contribution of each variable to the principal components.

All statistical analyses and data visualization were conducted using R software version 4.3.1 (R Core Team 2023).

Results

Diversity and taxonomic richness of soil macroarthropods

A total of 1420 specimens and 9048 individuals were processed. They were grouped into 23 taxonomic groups, seven classes, and 26 orders (Suppl. material 2). The Insecta class represented 72.86% of the specimens. Arachnida was the second most abundant class, representing 10.68% of the total specimens, followed by Chilopoda (5.9%), Diplopoda (5.3%), Diplura (2.9%), Malacostraca (2%), and Symphyla (0.5%).

From Insecta, Formicidae (ants) was the most abundant group (33.9%) and the group with the highest species richness (144 morphospecies). Blattodea,

Isoptera (termites) was the second most abundant group (15.8%) and the third in richness with 57 morphospecies. Coleoptera was the third most abundant group (7.48%) and the second one in richness with 70 morphospecies. From Arachnida, Araneae exhibit a high species richness with 56 morphospecies.

A total of 465 soil macroarthropod morphospecies were identified: 66 morphospecies in pastures, 171 morphospecies in young-age regrowth, 210 morphospecies in middle-age regrowth, and 241 morphospecies in old-growth fallows. The 46.6% of the morphospecies (288 msp) were collected only once, and 85% of the single occurrence abundances were found in regrowth stages (Suppl. material 2).

Sample-size-based rarefaction/extrapolation curves (Fig. 2) show the estimated species richness for each land use category. The predicted species values (Chao1) were 101 (± 19 SE) for pastures, 223 (± 22 SE) for young-age regrowth, 277 (± 25 SE) for middle-age regrowth, and 297 (± 21 SE) for old-growth fallows. These estimates show that species richness increases across time with differences in the species diversity of each fallow stage. The speed of diversity recovery decreases with time, being less after 11 years. As expected, pasture had the lowest diversity. A large number of taxonomic groups such as Pseudoscorpionida, Lepidoptera-larvae, Diplura, Diptera-larvae, Archaeognata, Scorpiones and Symphyla were reported since initial stages of regrowth. Taxonomic groups such as Ricinulei, Schizomida, and Orthoptera were not present at young stages, but were present at mature stages of regrowth (middle-age and old-growth).

The ant species *Tranopelta gilva* was the most abundant in the study area, representing 3.85% of the samples, followed by the termite *Anoplotermes meridianus* (2.49%) and the centipede *Ribautia* sp1 (1.64%). Other morphotypes with high relative abundance (over 1.5%) were Japygidae sp1, *Cylindrotermes parvignathus*, and *Wasmannia auropunctata*.

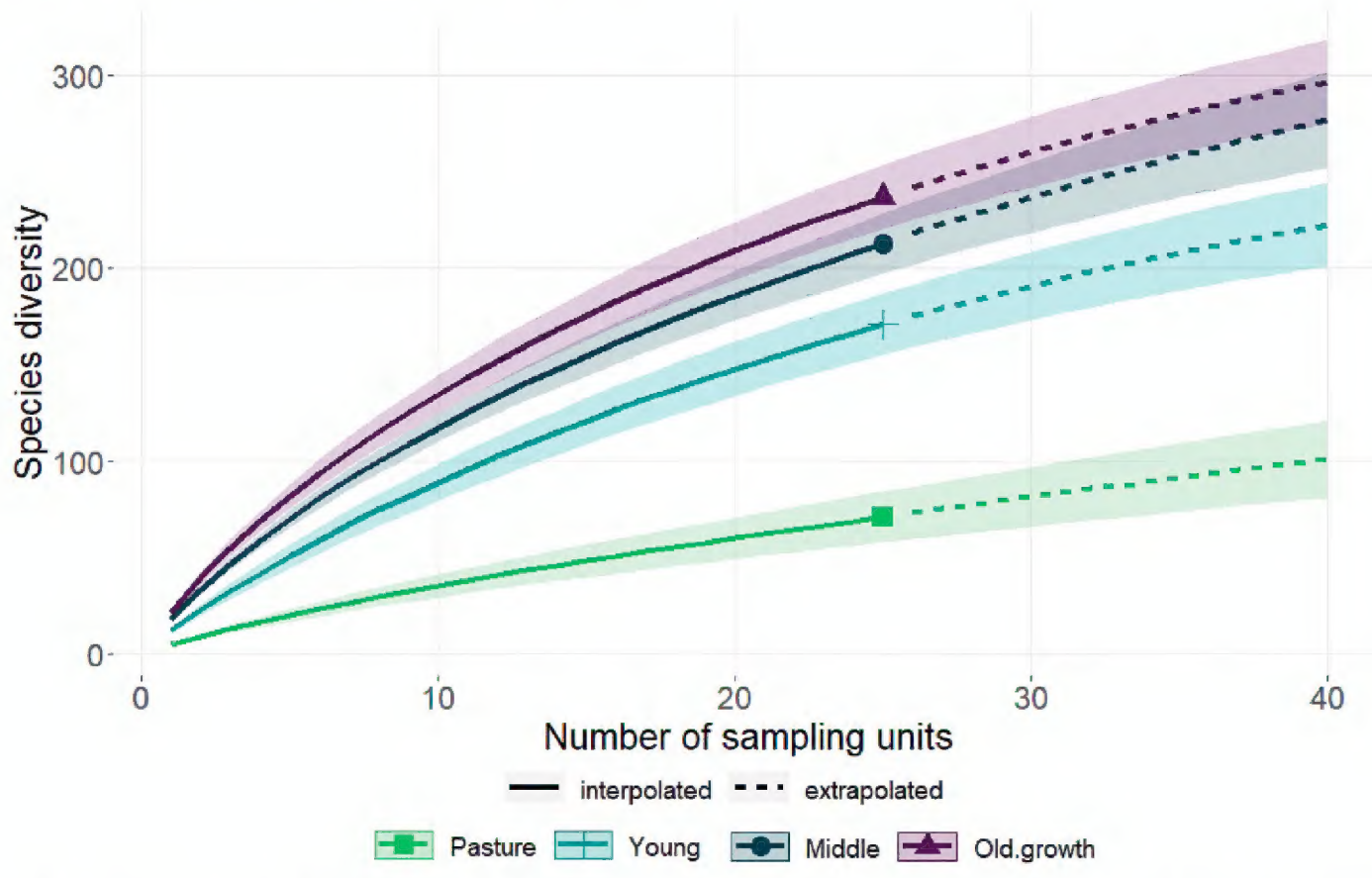

Figure 2. Sample-size-based rarefaction/extrapolation curves of soil macroarthropod diversity in pasture; young age (1 to 10 years); middle age (11 to 20 years); and old-growth age (21 to 30 years) fallows.

Density and mass of soil macroarthropods

Significant differences in the density and mass in alcohol of various macroarthropod taxa across different stages of natural regrowth occurred (Table 1). Eleven groups showed significant changes in density and eight groups exhibited significant changes in mass through the natural regrowth. The morphotypes that contributed the most to soil biomass were Scarabaeidae larvae. Seven groups displayed significant differences in both biomass and density across the regrowth stages, with *P*-values < 0.0001 for Araneae, Chilopoda, Diplopoda, Formicidae, and Isoptera, followed by Diplura and Coleoptera larvae. Twelve taxonomic groups (52% of the total) showed consistent patterns of stability in both density and mass in alcohol ($P > 0.01$) across different stages of the natural regrowth and represented 2.77% of the total biomass and 0.95% of the total density of the sampled soils.

A rapid recovery in density, biomass and species richness of soil macroarthropod communities was evident (Fig. 3). Pastures accounted for only 7.7% of the biomass and 2.6% of the density found across all sampling sites (Table 1). Blattodea sp3, Blattodea sp4, and Ctenidae sp2 had the highest biomass contributions in pasture soils. The ants *Crematogaster* cf. *acuta*, *Wadeura guianensis*, and *Nylanderia* sp1 contributed most to the macroarthropod density in pastures (Suppl. material 2.). In the early regrowth stage, density showed the greatest increase rising by up to 1150%, and biomass by 210% (Table 1). The old-growth age had the highest biomass and density compared to the other regrowth ages (52.83% and 45.54% of the total, respectively).

Ants (Formicidae) showed high densities in young-age sites and substantial biomass across all stages, peaking in middle-age sites (Suppl. material 2.). Chilopoda (centipedes) also increases density and biomass with regrowth age ($P < 0.0001$), and particularly in young-age and middle-age stages. Araneae (spiders) showed a significant increase in both density ($P = 0.0056$) and biomass ($P < 0.0001$), with the highest values observed in old-growth age sites. Blattodea (cockroaches and termites) and Isoptera (termites) exhibit significant biomass accumulation in old-growth age ($P < 0.0001$). Diplura and Coleoptera larvae densities increased with regrowth age, with Coleoptera larvae displaying a marked biomass peak in old-growth sites.

In the middle and old-regrowth ages, the highest biomass contribution was from the termite species *Syntermes territus*, *Neocapritermes utiariti*, and the spider Barychelidae sp4 (Suppl. material 2.). In middle and old regrowth ages social insects (ants and termites) morphospecies such as *Cyrilliotermes angulariceps*, Apicotermitinae sp2, *Rustitermes boteroi*, *Tranopelta gilva*, *Cylindrotermes parvignathus*, *Hydrecotermes kawaii*, and *Anoplotermes meridianus* contributed the most to macroarthropod densities (Suppl. material 2).

Vertical distribution patterns of macroarthropods

Changes in the vertical distribution of macroarthropod communities were evidenced through regrowth stages. The mass in alcohol and density of macroarthropods was significantly different at different soil depths ($P < 0.0001$) across all regrowth ages (Fig. 4A, C, Table 2). The 0–10 cm soil depth had the highest density and mass values across all ages. Although this pattern

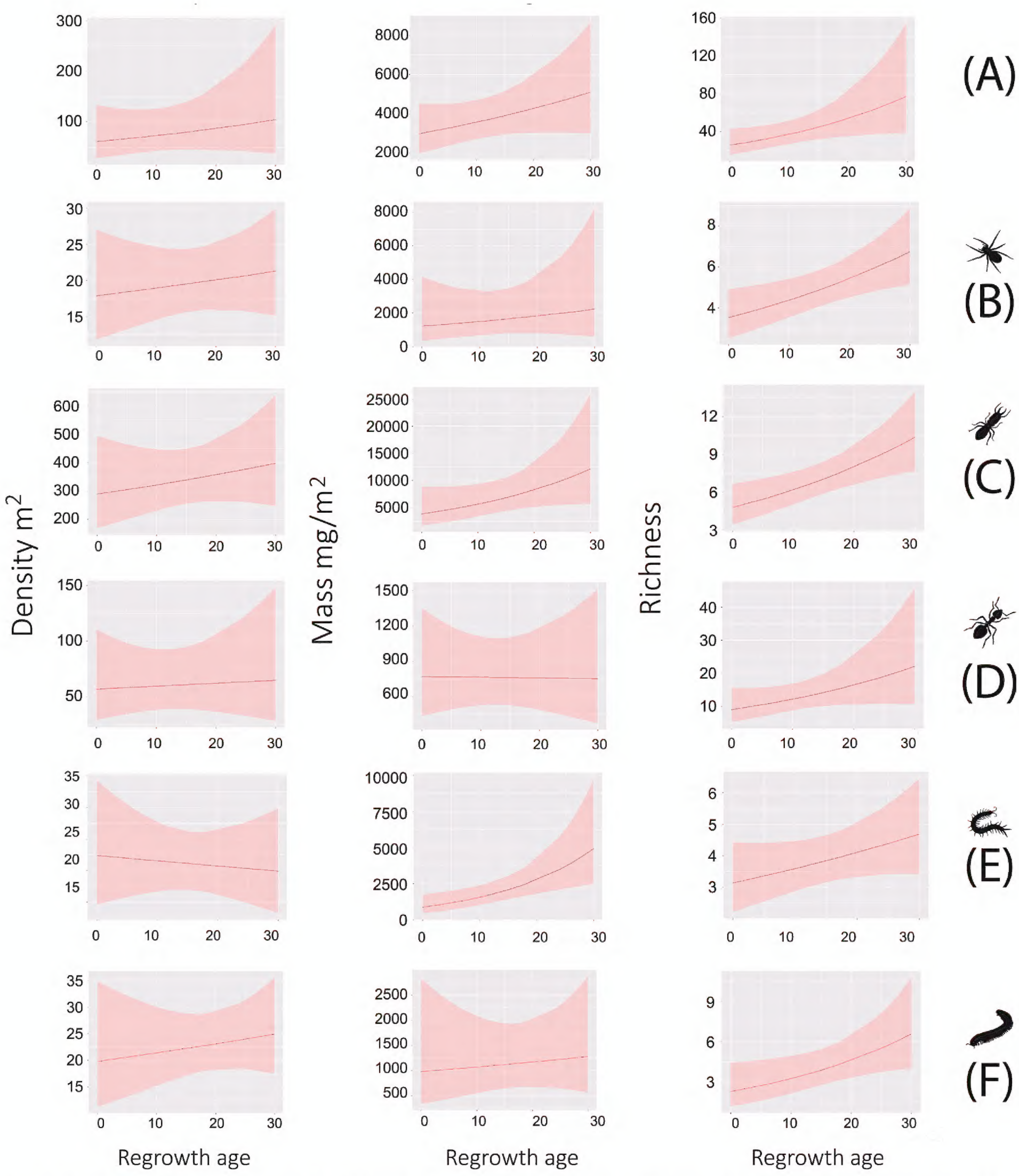

Figure 3. GLMM predictions (lines with 95% confidence intervals) showing changes of mean density ind/m2 (left), mass in alcohol mg/m2 (center) and richness (right) across natural regrowth ages in **A** total soil macroarthropods **B** Araneae – spiders **C** Isoptera – termites **D** Formicidae – ants **E** Chilopoda – centipedes **F** Diplopoda – millipedes.

was subtler in mass, it is evident how other groups as herbivores and predators can influence and change distribution patterns, particularly at older ages (Fig. 4B). Macroarthropod density was entirely driven by ecosystem engineers, with omnivores like ants influencing young regrowth stages and termites as decomposers in older stages.

Table 1. Differences of soil macroarthropod communities in plots with different natural regrowth ages at the Northwestern Amazon. Mean values followed by standard errors in parenthesis (n = 25). Significance values are indicated as follows: * = $P < 0.01$; ** = $P < 0.001$; *** = $P < 0.0001$. Different letters indicate significant differences ($P < 0.01$) among regrowth ages according to Fisher's LSD test.

Taxa group	Density (individuals/m²)					Mass in alcohol (mg/m²)				
	Pasture	Young-age	Middle-age	Old-growth age	*P*-value	Pasture	Young-age	Middle-age	Old-growth age	*P*-value
Araneae	7.04 (3.1) [b]	8.32 (3.6)[ab]	21.12 (9.2)[ab]	30.08 (13.1)[a]	**	50.8 (32.9)[c]	91.6 (59.4)[bc]	731 (473.9)[ab]	1631.6 (1057.1)[a]	***
Archaeognatha	0	0.64 (0.2)	0.67 (0.2)	2.46 (0.32)	0.999	0	0.8 (0.2)	9.6 (0.6)	8.4 (0.6)	0.99
Blattodea	8.32 (0.6)	1.92 (0.3)	5.12 (0.4)	6.4 (0.51)	0.83	299.6 (3.5)[a]	9.2 (0.61)[a]	807.6 (5.7)[ab]	1263.2 (7.1)[b]	**
Chilopoda	3.2 (1.3)[b]	14.72 (5.7)[a]	29.44 (11.4)[a]	23.04 (8.9)[a]	***	23.6 (12.6)[b]	84.4 (45.1)[a]	252.59 (135)[a]	920.4 (497.7)[b]	***
Coleoptera	11.52 (0.7)[a]	20.48 (0.9)[b]	29.44 (1)[c]	19.84 (0.9)[b]	*	45.6 (26.5)	287.47 (165.4)	248.78 (143.2)	149.2 (85.89)	0.071
Dermaptera	2.56 (0.3)	1.92 (0.3)	0	0.64 (0.2)	0.999	12.8 (14.9)	251.46 (293.8)	56.19 (65.7)	4.4 (5.16)	0.189
Diplopoda	1.28 (0.7)[b]	4.48 (2.4)[b]	29.44 (15.7)[a]	35.84 (19.1)[a]	***	23.2 (16.3)[b]	11.46 (8.1)[b]	256 (179.3)[a]	236 (165.2)[a]	***
Diplura	0[b]	5.76 (0.5)[b]	6.4 (0.51)[b]	23.04 (0.96)[a]	*	0[a]	34.4 (23.71)[b]	8.06 (5.6)[ab]	35.8 (24.6)[b]	*
Formicidae	86.4 (23.2)[a]	627.2 (167.8)[b]	483.84 (129.5) [b]	370.56 (99.2) [b]	***	106.98 (30.6)[a]	607.6 (173.7)[b]	743.8 (210)[b]	493.2 (141)[b]	***
Hemiptera	1.92 (1.1)[b]	11.52 (6.7)[a]	23.68 (13.8)[a]	13.44 (7.9)[a]	**	6.8 (5.5)	203.12 (162.5)	1010.26 (808)	424 (339.1)	0.161
Isopoda	3.2 (0.4)[a]	1.92 (0.3)[a]	7.68 (0.55)[b]	8.96 (0.6)[b]	*	2 (1.7)	3.2 (2.8)	11.79 (10.2)	10.38 (8.9)	0.787
Blattodea: Isoptera	4.48 (1.7)[a]	1031.04 (382.6)[b]	731.2 (271.4)[b]	1855.6 (688.6)[b]	***	2.8 (1.16)[b]	2787.6 (1103.7)[a]	1438 (569.4)[a]	6293.6 (2491.8)[a]	***
Coleoptera-larvae	14.72 (5.7)[a]	10.88 (4.2)[a]	25.6 (9.9)[b]	21.12 (8.2)[b]	*	1512.8 (916.4)[ab]	232.6 (140.9)[b]	451.6 (273.6)[a]	2732.8 (1655.5)[a]	*
Diptera-larvae	0	1.28 (0.2)	3.2 (0.36)	1.28 (0.23)	0.998	0	77.6 (1.76)	232.8 (3.1)	0.53 (0.1)	0.99
Hymenoptera-larvae	5.12 (0.2)	0	0	0	0.998	46 (0.01)	0	0	0	0.99
Lepidoptera-larvae	0	1.28 (0.2)	0.64 (0.16)	2.56 (0.32)	0.998	0	17.2 (0.8)	12.8 (0.7)	54.8 (1.5)	0.99
Opiliones	0.64 (0.4)[a]	7.68 (5.3)[b]	6.4 (4.43)[b]	12.16 (8.39)[b]	*	4.4 (4.21)	1291.6 (1229.3)	17.79 (16.9)	91.6 (87.2)	0.761
Orthoptera	0	0	2.56 (0.32)	2.56 (0.32)	0.999	0	0	54.4 (1.48)	151.2 (2.5)	0.705
Pseudoscorpionida	0	3.84 (0.4)	4.48 (0.42)	8.96 (0.6)	0.941	0	2.19 (2.1)	47.6 (44.8)	5.46 (5.2)	0.563
Ricinulei	0	0	0	0.64 (0.2)	0.941	0	0	0	0.4 (0.1)	0.563
Schizomida	0	0	0	1.28 (0.2)	0.999	0	0	0	1.2 (0.22)	0.563
Scorpiones	0	0.64 (0.1)	0.64 (0.16)	0	0.999	0	13.2 (0.7)	31.2 (1.12)	0	1
Symphyla	0	2.56 (0.3)	0.64 (0.16)	1.92 (0.3)	0.999	0	0.32 (0.38)	0.06 (0.1)	0.32 (0.38)	0.969

The mass in alcohol between litter and the 10–20 cm depth did not differ significantly across the regrowth stages; differences were only found in pastures ($P < 0.001$), while no significant differences were observed at other ages ($P > 0.01$). However, in the old-growth forest, the 10–20 cm layer showed an increase in its mean values, even surpassing the 0–10 cm layer but without presenting significantly differences, due to the presence of

Table 2. Vertical distribution differences in soil macroarthropod communities in plots with different natural regrowth ages at the Northwestern Amazon. Mean values followed by standard errors in parenthesis (n = 25). Significance values are indicated as follows: *** = $P < 0.0001$. Different letters indicate significant differences ($P < 0.01$) among regrowth ages according to Fisher's LSD test.

Depth	Density (individuals/m2)				*P*-value	Mass in alcohol (g/m2)				*P*-value
	Pasture	Young-age	Middle-age	Old-growth age		Pasture	Young-age	Middle-age	Old-growth age	
Litter	32 (7.44)^{a}	303.36 (98.89)^{b}	455.04 (156.53)^{b}	625.92 (172.14)^{b}	***	0.343 (0.14)^{a}	0.622 (0.23)^{ab}	1.489(0.45)^{bc}	3.298 (0.88)^{c}	***
0-10 cm	78.08 (35.03)^{a}	1051.52 (223.41)^{b}	631.04 (94.82)^{c}	1304.32 (233.75)^{b}	***	1.693 (0.83)^{a}	2.733 (0.91)^{ab}	3.356 (0.79)^{b}	5.337 (1.3)^{b}	0.0083
10-20 cm	30.08 (10.78)^{a}	269.44 (119.36)^{b}	272.64 (75.11)^{c}	417.92 (112.25)^{c}	***	0.068 (0.01)^{a}	0.768 (0.49)^{b}	1.229 (0.4)^{c}	5.085 (2.47)^{d}	***
20-30 cm	12.13 (3.72)^{a}	138.24 (56.86)^{ab}	47.36 (17.04)^{a}	111.36 (39.99)^{b}	0.0036	0.034 (0.01)^{a}	0.372 (0.16)^{a}	0.233 (0.08)^{a}	0.786 (0.52)^{b}	0.0014

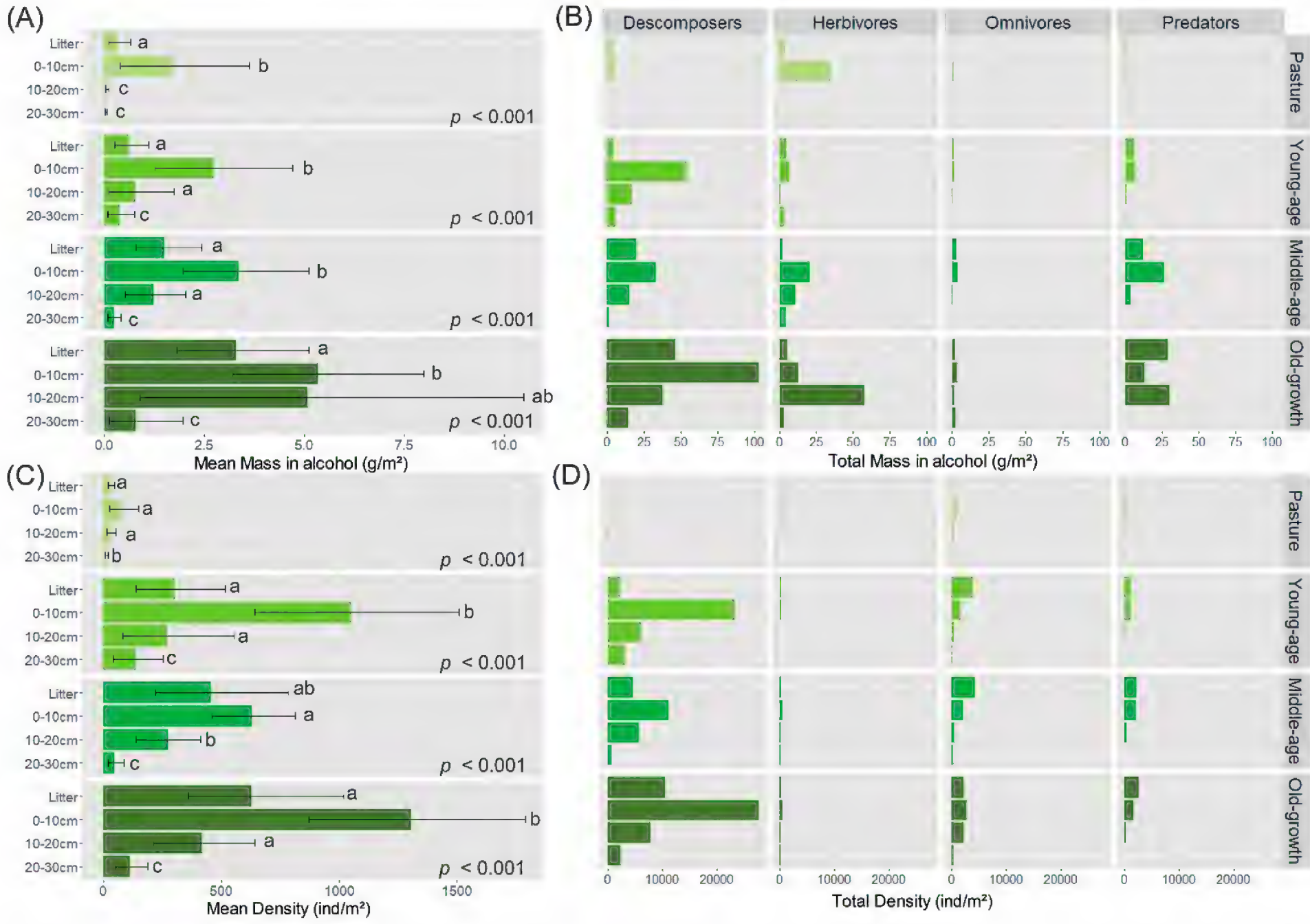

Figure 4. Vertical distribution of soil macroarthropod communities across natural regrowth stages (Up to down pasture, young-age, middle-age, and old-growth fallows) **A** mean with std. error of mass in alcohol **B** total mass in alcohol (g/m^2) by feeding guilds **C** mean with std. error of density **D** total density (individuals/m^2) by feeding guilds. Different lower case letters indicate a significant difference ($P < 0.01$) among soil depths according to Fisher's LDS test.

large-bodied species (Scarabaeidae larvae, *Syntermes territus*, and Barychelidae sp4, Suppl. material 2). The composition of the litter also differs from that at the 10–20 cm depth. Omnivores and predators are more dominant in the litter, while herbivores are more dominant at the 10–20 cm depth. Among ecosystem engineers, their composition also differs between the two layers. Ants account for up to 33.7% of their density in the litter, while at 10–20 cm

they represent 20.2%, compared to 17% for termites both in the litter and at 10–20 cm depth. Notably, 60% of termites are concentrated only at 0–10 cm depth, where ants represent less than 40% of density and mass.

Among all soil depths, the 20–30 cm soil depth consistently differed from the others, showing the lowest values for both mass and density across all regrowth stages. In old-regrowth, the 0–10 cm soil depth represents more than 50% of the biomass and over 35% of the density while the 20–30 cm soil depth accounts less than 5% of the biomass and less than 4.5% of the density of that stage.

Soil physicochemical characteristics

Soil properties changed across the different stages of natural regeneration (Table 3). Pasture soils had higher bulk densities, higher electrical conductivity, and higher amounts of P, Cu, and Zn. Those variables decreased through the natural regrowth. At the same time, cation exchange capacity, organic carbon (OC), and Ca increased through the natural regrowth. Some trends, without statistical significance, were also observed in the depth of horizons O and A increasing with the age of the regrowth.

Additionally, sodium levels were significantly higher in the more advanced regeneration stages, while phosphorus levels were lower. Copper and zinc showed significant decreases with age, whereas boron and iron did not exhibit significant changes, despite variations in concentration. Overall, soil quality improved in more advanced stages of natural regeneration, marked by higher organic carbon and lower bulk density.

Table 3. Soil properties in plots with different natural regrowth ages at the Northwestern Amazon. Mean values followed by standard errors in parenthesis (n = 5). Significance values are indicated as follows: * = $P < 0.01$; ** = $P < 0.001$; *** = $P < 0.0001$. Different letters indicate significant differences ($P < 0.01$) among regrowth ages according to Fisher's LSD test.

Soil Variable	Regrowth age				*P*-value
	Pasture	Young-age	Middle-age	Old-growth age	
O horizon (OH)	1.8 (0.1)a	2.36 (0.435)ab	3.8 (0.487)b	4.5 (0.138)b	0.163
A horizon (AH)	6.0 (1.772)	8.7 (1.722)	12.28 (1.412)	14.1 (1.699)	0.208
Clay (%)	20.2 (4.841)	29.6 (7.973)	33.046 (7.254)	37.468 (9.042)	0.602
Sand (%)	47.8 (8.766)	64.444 (7.437)	59.334 (7.911)	55.09 (9.798)	0.393
Silt (%)	32 (4.561)^{a}	5.954 (0.903)^{b}	7.622 (1.126)^{b}	7.444 (0.873)^{b}	***
Bulk density (g/cm3)	1.302 (0.015)^{a}	1.302 (0.043)^{a}	1.192 (0.067)^{a}	1.064 (0.052)^{b}	*
pH	4.174 (0.214)	4.552 (0.071)	4.626 (0.176)	4.55 (0.055)	0.252
Electrical conductivity (dS/m)	0.416 (0.125)^{a}	0.16 (0.033)^{b}	0.224 (0.044)^{b}	0.234 (0.071)^{b}	***
Cation exchange capacity (meq/100 g)	3.368 (0.46)	4.474 (0.94)	6.902 (1.235)	5.598 (1.325)	0.052
Organic carbon (%)	1.088 (0.135)^{a}	1.15 (0.116)^{b}	1.266 (0.069)^{bc}	1.684 (0.090)^{c}	**
Total nitrogen (%)	0.168 (0.04)	0.08 (0.006)	0.104 (0.006)	0.114 (0.06)	0.11
K (mg/kg)	42.9 (15.842)	29.074 (4.153)	57.128 (12.392)	43.38 (7.644)	0.147
Ca (mg/kg)	184.6 (14.579)	224.222 (9.225)	247.122 (12.392)	216.546 (5.649)	0.041
Na (mg/kg)	29.32 (0.58)^{a}	38.89 (3.911)^{b}	45.576 (1.177)^{c}	41.064 (3.023)^{bc}	***
Fe (mg/kg)	454 (145.897)	550.754 (67.098)	391.734 (68.858)	377.09 (48.315)	0.302
Cu (mg/kg)	2.34 (0.402)^{a}	1.43 (0.099)^{bc}	1.444 (0.18)^{b}	0.908 (0.2)^{c}	**
Zn (mg/kg)	2.96 (0.521)^{a}	0.782 (0.098)^{b}	1.316 (0.24)^{c}	0.902 (0.178)^{b}	***
B (mg/kg)	0.112 (0.028)	0.216 (0.07)	0.242 (0.061)	0.242 (0.083)	0.395
P (mg/kg)	4.086 (1.341)^{a}	2.76 (0.182)^{b}	3.114 (0.191)^{b}	2.784 (0.379)^{b}	***

Correlations between soil physicochemical characteristics and macroarthropod assemblages

The principal component analysis (Fig. 5) reveals a segregation of soil macroarthropod communities and soil physicochemical variables across different natural regrowth stages. PCA axis 1 explained 38% of the total variation, while PCA axis 2 explained 10.6%, accounting for 48.6% of the variation in total (RV = 0.448). The significance of the results was further supported by a Monte Carlo test, which yielded a *P*-value of 0.001, indicating a highly significant differentiation. From the correlation of the variables explored in PC1 and PC2, several key patterns emerge (Suppl. material 3). PC1 shows strong positive correlations with density (0.878, $P < 0.0001$), richness (0.934, $P < 0.0001$), ecosystem engineers (0.853, $P < 0.0001$), Isoptera (0.761, $P < 0.0001$), and decomposers (0.796, $P < 0.0001$). Negative correlations with variables such as silt (-0.774, $P < 0.0001$), phosphorus (-0.819, $P < 0.0001$), and zinc (-0.783, $P < 0.001$) suggest that higher levels of these elements are inversely related to the main variation captured by PC1.

In contrast, PC2 showed significant positive correlations with bulk density -(0.601, $P < 0.01$), and organic carbon (0.592, $P < 0.01$). The feeding guilds and taxonomic groups were differentially distributed along the PCA axes, indicating distinct ecological affinities and responses to soil conditions and regrowth stages. Old-growth forests are strongly correlated with biotic variables such as mass, richness, density, predators, and ecosystem engineers, indicating that more mature soils have greater diversity and abundance of soil organisms. Middle-aged and young-age fallows, also related to biotic variables, in this case as decomposers and omnivorous, showed progress towards maturity with increasing macroarthropod diversity but did not reach the complexity of old-growth soils.

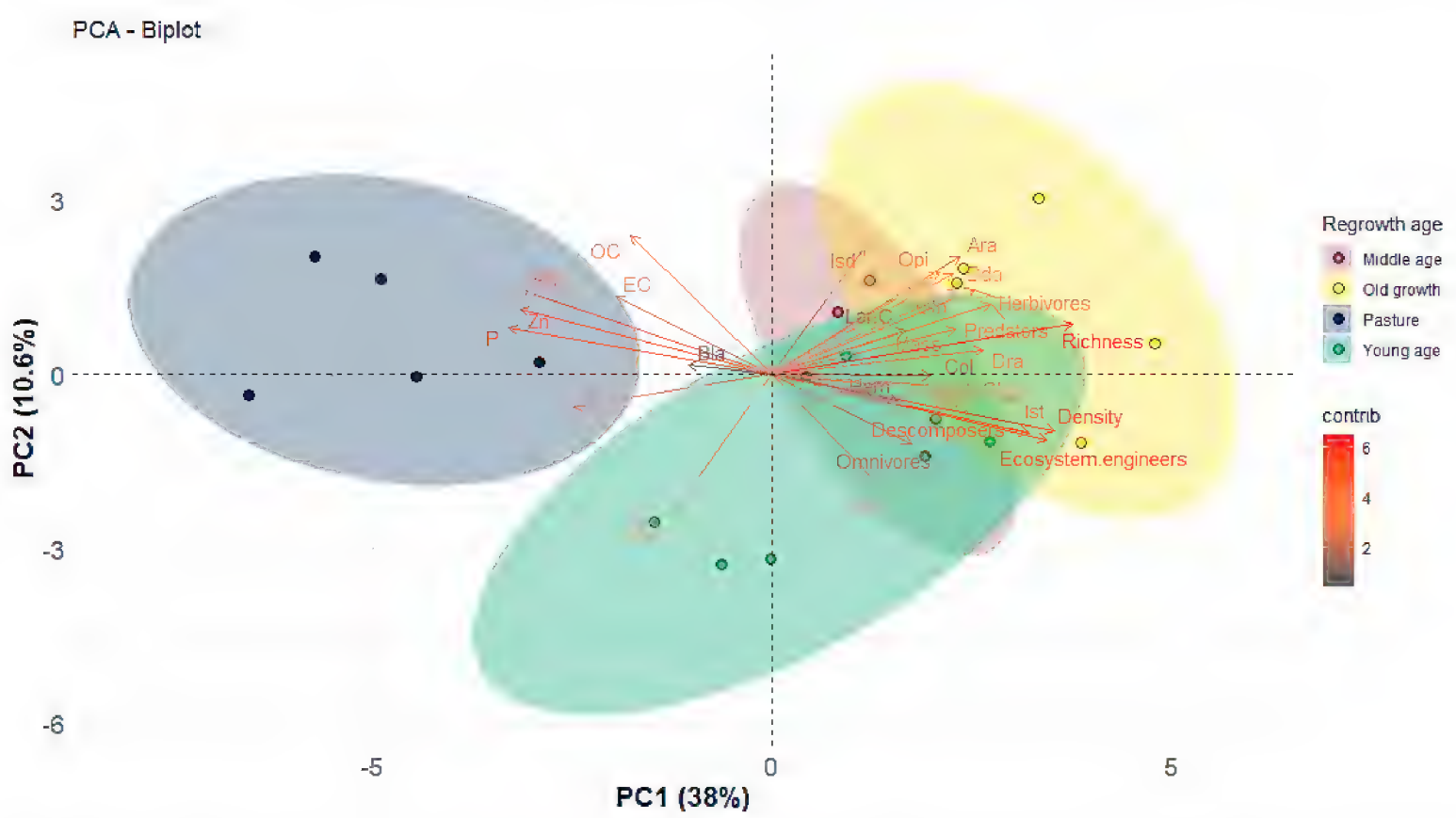

Figure 5. Principal Components Analysis ordination map of density, biomass, richness, feeding guilds, main soil macroarthropod taxa groups with soil physicochemical variables across natural regrowth stages (*P*-value = 0.001 by Monte-Carlo test, based on 999 permutations; RV = 0.448). Araneae (Ara), Bulk density (BD), Blattodea (Bla), Chilopoda (Chi), Coleoptera adults (Col), Copper (Cu), Diplopoda (Dda), Diplura (Dra), Electric conductivity (EC), Formicidae (For), Hemiptera (Hem), Isopoda (Isd), Isoptera (Ist), Coleoptera larvae (Lar.C), Sodium (Na), Organic Carbon (OC), Opiliones (Opi), Other taxa-groups (Otr), Phosphorous (P), Zinc (Zn). The color gradient represents the varying levels of each variable's contribution to the component axes.

Pastures are associated with physicochemical characteristics such as higher bulk density, electrical conductivity, and elevated concentrations of phosphorus and zinc. These conditions suggest lower diversity and abundance of macroarthropod compared to more mature soils. Young-age soils, characterized by similar correlations with bulk density and other physicochemical variables, exhibited high macroarthropod density, driven by ecosystem engineers reaching densities of up to 3888 individuals per m^2, although with lower diversity compared to older regrowth stages. In contrast, older regrowth stages, characterized by improved soil conditions over time, supported greater mass, as well as taxonomic and trophic diversity, of soil macroarthropod communities.

Discussion

Natural regrowth of pastures increases macroarthropod diversity, mass, and density, but recovery patterns varied significantly among different groups. Ants and some Coleoptera dominate early regrowth stages, while predators like spiders and centipedes increased after 20 years. After 30 years, ecosystems showed a good nutrient accumulation and a complex community with termites leading it. Macroarthropod vertical distribution also changes, with the dominance of ants in the litter and termites in the topsoil. These results highlight the complex soil recovery process mediated by soil macroarthropods.

Pastures seem to be a different environment when compared to fallows, independent of their age, with an increased bulk density (Carneiro et al. 2009; Beylich et al. 2010; Cherubin et al. 2019) that is associated with more compacted soils (Sharrow 2007), and that is unfavorable for most soil macroarthropods. Pastures also have high levels of zinc (Zn) and copper (Cu) that could be toxic (Van Zwieten et al. 2004; Hill and Shannon 2019), and could affect ants and earthworm diversity (Diehl et al. 2004; Sofo et al. 2020). Herbivores dominated the grasses with high mass and abundance, mainly represented by beetle larvae, which resist soil compaction and prefer to consume the roots of grass and young trees (De Farias and Hernández 2017). These findings align with Duran-Bautista et al. (2023), who reported increased wireworms, a type of soil-dwelling herbivorous beetle larvae (Coleoptera, Elateridae), within a pasture land of the Amazon region. The high herbivores mass in pastures occur by the presence of large Scarabaidae larvae at 0–10 cm depth, which are considered pests in some cases (Roberts and Morton 1985; Casas et al. 2021). However, ant species such as *Wasmannia auropunctata*, *Crematogaster* cf. *acuta*, *Acropyga exsanguis* and *Wadeura guianensis* seems to be adapted to it. Macroarthropod densities and mass were lower in pastures than in fallows. The group that exhibited higher densities and mass in pastures was ants, as reported previously (Rodríguez et al. 2021b).

The main feeding guild associated with pastures consists of herbivores that predominantly feed on grasses. Here, P concentrations and other minerals were significantly high, indicating additional sources of organic matter (such as cattle manure). N concentrations in soil pastures were higher than in fallows, contrary to what has been reported in other works (Lepage et al. 2006, de Paula et al. 2016). Although termites can increase N soil availability (Ndiaye et al. 2004; Fallah et al. 2017; Ashton et al. 2019), in our study area termites were not important in pastures. Thus, soil N availability could be the result of earthworm (Gonzalez and Zou 1999; Domínguez et al. 2004) and ant metabolism (Evans

et al. 2011) of livestock urine and manure. In general, pasture soil is a poor environment in terms of macroarthropod diversity. There, where soil compaction is evident, only the biomass of Coleoptera larvae was significant (Sharrow 2007). At 10–20 cm depth macroarthropod biomass increased by Coleoptera larvae, Araneae, and Isoptera. At 20–30 cm soil depth, the number of taxonomic groups decreased with soil depth (Pauli et al. 2011; Ayuke et al. 2019). Pastures indirectly reduce predator mass by favoring invertebrate herbivory and omnivores in livestock grazing plots (Moran and Hurd 1997; Farrell et al. 2015).

As natural regeneration occurs, more organic matter comes from a more stratified covering increasing the thickness of litter layer (Horizon O) (De Carvalho Balieiro et al. 2008). Litter, thus, will provide more sources of food for a more diverse macroarthropod community. The highest macroarthropod density and mass occurred at 0–10 cm depth, dominated by termites, particularly those of the subfamily Apicotermitinae. Ecosystem engineers, particularly termites, played a crucial role in the composition of macroarthropod communities (Bignell and Eggleton 2000). Soil macroarthropod diversity increased considerably in the early stages of natural regrowth, suggesting a rapid recovery of soil fauna diversity in the first years after pasture abandonment (Meloni and Varanda 2015; Amazonas et al. 2018). Although young fallows had high diversity and abundance, mature fallows were where most macroarthropod groups truly recovered and stabilized after around 30 years (Serra et al. 2021). Initially, these first changes in the soil are driven by ants (Formicidae), termites (Blattodea, Isoptera) as they were the most abundant organisms, and presumably earthworms (Frouz 2024) that were not evaluated in this study. Furthermore, it is important to highlight that some species of ants and termites, classified in the four guilds evaluated, were ecosystem engineers, which highlights the crucial importance of these species in the composition and structure of these communities (Donovan et al. 2001; Wilkie et al. 2010; Brandão et al. 2012). This group encompasses a diversity of diets, highlighting their fundamental role in ecosystem dynamics.

The litter layer presented the highest abundance of macroarthropods, primarily due to the high density of ants, common in Amazon soils (Wilkie et al. 2010; Castro et al. 2018). Termite density increases from 3% to more than 75% along the natural regrowth while ant density did not change through time. Despite the overall increase in diversity through natural regrowth, some species that were abundant in pastures and young fallows became less prevalent in old-growth fallows, in response to a reduction of food for herbivores (Feldpausch et al. 2005; Klink et al. 2015; Mesquita et al. 2015). Generalist and open-habitat specialist ants that dominate grasslands were replaced by up to 41% more ant species in the first 10 years of regeneration. Species such as *Wasmannia auropunctata*, which bloom in pastures (Solar et al. 2016), being one of the three dominant species in pastures, were replaced by up to 32 ant species in the old regrowth.

Decomposers such as Diplopoda are highly susceptible to ecosystem disturbances (Barros et al. 2001; Cerón et al. 2008; Marchão et al. 2009), but its recovery started with regrowth when the forest structure begins to change considerably (Caron et al. 2021). Isopoda also shows changes in density and biomass along the regrowth, but without significant changes in mass, suggesting that it is more sensitive to agrochemicals and soil acidification than to soil compaction or nutrient limitation (Snyder and Hendrix 2008; Menta 2012; Souty-Grosset and Faberi 2018). Non-termite Blattodea (cockroaches) mass increasing up

to 76% in old regrowth (although their density did not, $p = 0.83$), being groups susceptible to forest disruption due to the need of leaf litter (Donoso et al. 2010). Additionally, open areas act as dispersal barriers for macroarthropods, making the forest a refuge for these groups (Evangelista et al. 2017).

Araneae, Blattodea, and Coleoptera-larvae which are also sensitive to land-use changes (Marchão et al. 2009; Araújo et al. 2010; de Vasconcelos et al. 2020), increased their mass along with natural regrowth. In forested soils, termites contributed more to macroarthropod density and biomass than other groups. Termites are well-documented for their role in enhancing soil fertility (Jouquet et al. 2011, 2014; Duran-Bautista et al. 2020), directly and positively influencing soil quality (Rodríguez-León et al. 2021). Termites biomass increased from 0.12% in pastures to 43% in old-regrowth stages, as reported by Dahlsjö et al. (2014), highlighting the notable contribution to global animal biomass (Tuma et al. 2020). Calcium (Ca) and sodium (Na) were more abundant in middle and old-growth fallows. Termites have been reported as mediators of soil Ca and Na availability (Sanabria et al. 2016; Castro et al. 2021), released those into the soil in the areas where termite mounds are present (Schaefer et al. 2016; Lima et al. 2018). These enriched soil patches will attract other groups such as leaf litter arthropods (Barros et al. 2002) and Isopoda and Diplopoda (Cromack et al. 1977), which are usually favored by high levels of soil macronutrients.

Chilopoda and Diplopoda mass was higher in old-growth stages, being more abundant in forests (Barros et al. 2001). Interestingly, Chilopoda showed high mass despite a low number of species, while Diplopoda exhibited high mass with high species richness. This indicates that Diplopoda could be more diverse in secondary Amazon forests (Demetrio et al. 2021). Chilopoda diversity is more related to the level of forestation and canopy cover (Ruiz et al. 2008; Amazonas et al. 2018). However, GLMM prediction model indicated a negative balance over the years for Chilopoda related to a density decrease; this can be interpreted as a result of their lower density due the increase of the other groups (Höffer et al. 2001; Serra et al. 2021), such as Araneae and even predatory ants (Dambros et al. 2016; Sofo et al. 2020).

Results indicated that deeper soil layers (below 20 cm depth) provide significant insights into taxonomical and functional changes, but are often overlooked (Moradi et al. 2020). The high macroarthropod density in middle-age and old-growth fallows provided a good food supply for predators (Araújo et al. 2010; Guimarães et al. 2020; Pollierer et al. 2021). Thus, density and mass of Predators, including Araneae, Chilopoda, Diplura (Japygidae) and some Opiliones and Coleoptera, recovered significantly through natural regrowth, with new predator species appearing in older fallows (Cole et al. 2016, 2019; Serra et al. 2021). Japygidae, a little-known family, responded positively to natural ecosystem restoration (Botina et al. 2012, de Vasconcelos et al. 2020).

The interaction between the biotic and abiotic components of the soil is essential for maintaining a balanced and productive ecosystem (Briones 2018; Brown et al. 2018). The clear segregation of taxonomic groups and feeding guilds and their relation to regrowth age, confirms the recovery of soil macroarthropod in the study area (Rodríguez et al. 2021a, Duran-Bautista et al. 2023). Our study did not include earthworms which might change the patterns here exposed in terms of the importance of each group as an ecosystem engineer but not the general patterns here presented (Conrado et al. 2023; Bartz et al. 2024;

Brown et al. 2024). Results indicated that abiotic edaphic variables were segregated at the young regrowth stages, but soil health seems to be more linked to biotic variables (Castro et al. 2021; Rodríguez-León et al. 2021), demonstrating the importance of monitoring of soil biological communities to secure the complete recovery of ecosystem and not only some components of it.

Conclusion

Natural regrowth, considered a passive restoration strategy, is an alternative to enhance the diversity, density, and biomass of soil macroarthropod communities. Within the first 10 years, there is a rapid increase in diversity and abundance, dominated by ants and termites in compacted soils rich in phosphorus and zinc. Over subsequent decades, diversity continues to rise, accompanied by gradual improvements in soil quality and ecosystem complexity, with termites and predators such as spiders, becoming more prominent. Vertical distribution also shifts during regrowth, with ants dominating litter in pastures and termites dominating the upper soil layers of fallows, where decomposition processes are most active. These findings suggest the need for further research to understand the ecological processes driving these patterns and to explore how passive restoration strategies can support long-term recovery and resilience in tropical ecosystems.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization, D.C., C.P.P.V., C.H.R. and A.S.; methodology, D.C., C.P.P.V., C.H.R. and A.S.; software, D.C., E.H.D.B. and A.S.; validation, D.C., C.P.P.V. and A.S.; formal analysis, D.C., C.P.P.V., A.S; investigation, D.C., C.P.P.V., C.H.R. and A.S; resources, C.H..R and A.S.; data curation, D.C..; writing—original draft preparation, D.C.; writing—review and editing, D.C., C.P.P.V., C.H.R, E.H.D.B. and A.S; visualization, D.C.; supervision, C.P.P.V. and A.S..; project administration, C.P.P.V. and C.H..R; funding acquisition, C.P.P.V. and C.H.R. All authors read and approved the final version of the manuscript

Author ORCIDs

Daniel Castro https://orcid.org/0000-0002-5060-6129
Clara P. Peña-Venegas https://orcid.org/0000-0001-6317-3767
Carlos H. Rodríguez-León https://orcid.org/0000-0002-4409-7495
Ervin H. Duran-Bautista https://orcid.org/0000-0002-4155-6350
Armando Sterling https://orcid.org/0000-0002-9955-9175

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Reference

Acioli ANS, Constantino R (2015) A taxonomic revision of the neotropical termite genus Ruptitermes (Isoptera, Termitidae, Apicotermitinae). Zootaxa 4032(5): 451–492. https://doi.org/10.11646/zootaxa.4032.5.1

Acosta LE, Machado G (2007) Diet and Foraging. In: Pinto-da-Rocha R, Machado G, Giribet G (Eds) Harvestmen: The Biology of Opiliones. Harvard University Press, Cambridge, MA and London, England, 309–338. https://doi.org/10.4159/9780674276833

Adis J (2002) Amazonian Arachnida and Myriapoda : identification keys to all classes, orders, families, some genera, and lists of known terrestrial species. Pensoft, 590 pp. https://search.worldcat.org/title/813287808 [March 8, 2024]

Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M (2013) Deforestation and Reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45(2): 262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x

Amazonas NT, Viani RAG, Rego MGA, Camargo FF, Fujihara RT, Valsechi OA (2018) Soil macrofauna density and diversity across a chronosequence of tropical forest restoration in southeastern Brazil. Brazilian Journal of Biology 78(3): 449–456. https://doi.org/10.1590/1519-6984.169014

Anderson JM, Ingram J (1993) Tropical soil biology and fertility: a handbook of methods. 2nd edn. CAB International, Wallingford.

Andriuzzi WS, Wall DH (2018) Soil biological responses to, and feedbacks on, trophic rewilding. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 373(1761): 20170448. https://doi.org/10.1098/rstb.2017.0448

Anthony MA, Bender SF, van der Heijden MGA (2023) Enumerating soil biodiversity. Proceedings of the National Academy of Sciences of the United States of America 120(33): e2304663120. https://doi.org/10.1073/pnas.2304663120

Araújo VFP, Bandeira AG, Vasconcellos A (2010) Abundance and stratification of soil macroarthropods in a Caatinga Forest in Northeast Brazil. Brazilian Journal of Biology 70(3 suppl): 737–746. https://doi.org/10.1590/S1519-69842010000400006

Armenteras D, Cabrera E, Rodríguez N, Retana J (2013) National and regional determinants of tropical deforestation in Colombia. Regional Environmental Change 13(6): 1181–1193. https://doi.org/10.1007/s10113-013-0433-7

Ashton LA, Griffiths HM, Parr CL, Evans TA, Didham RK, Hasan F, Teh YA, Tin HS, Vairappan CS, Eggleton P (2019) Termites mitigate the effects of drought in tropical rainforest. Science 363(6423): 174–177. https://doi.org/10.1126/science.aau9565

Ayuke FO, Kihara J, Ayaga G, Micheni AN (2019) Conservation agriculture enhances soil fauna richness and abundance in low input systems: Examples from Kenya. Frontiers in Environmental Science 7: 97. https://doi.org/10.3389/fenvs.2019.00097

Barros E, Curmi P, Hallaire V, Chauvel A, Lavelle P (2001) The role of macrofauna in the transformation and reversibility of soil structure of an oxisol in the process of forest to pasture conversion. Geoderma 100(1–2): 193–213. https://doi.org/10.1016/S0016-7061(00)00086-0

Barros E, Pashanasi B, Constantino R, Lavelle P (2002) Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biology and Fertility of Soils 35(5): 338–347. https://doi.org/10.1007/s00374-002-0479-z

Barros E, Grimaldi M, Sarrazin M, Chauvel A, Mitja D, Desjardins T, Lavelle P (2004) Soil physical degradation and changes in macrofaunal communities in Central Amazon. Applied Soil Ecology 26(2): 157–168. https://doi.org/10.1016/j.apsoil.2003.10.012

Bartz MLC, Dudas RT, Demetrio WC, Brown GG (2024) Earthworms as soil health indicators in no-tillage agroecosystems. European Journal of Soil Biology 121: 103605. https://doi.org/10.1016/j.ejsobi.2024.103605

Bates D, Maechler M, Bolker B, Walker S, Bojesen RH, Singmann H, Dai B, Scheipl F, Grothendieck G, Green P, Fox J, Bauer A, Krivitsky PN (2021) Package lme4: Linear Mixed-Effects Models using "Eigen" and S4. Package version: 1.1-27.

Benito NP, Brossard M, Pasini A, Guimarães MDF, Bobillier B (2004) Transformations of soil macroinvertebrate populations after native vegetation conversion to pasture cultivation (Brazilian Cerrado). European Journal of Soil Biology 40(3–4): 147–154. https://doi.org/10.1016/j.ejsobi.2005.02.002

Beylich A, Oberholzer HR, Schrader S, Höper H, Wilke BM (2010) Evaluation of soil compaction effects on soil biota and soil biological processes in soils. Soil & Tillage Research 109(2): 133–143. https://doi.org/10.1016/j.still.2010.05.010

Bignell DE, Eggleton P (2000) Termites in Ecosystems. Termites: Evolution, Sociality, Symbioses, Ecology. Springer Netherlands, 363–387. https://doi.org/10.1007/978-94-017-3223-9_17

Borges FLG, Oliveira M da R, de Almeida TC, Majer JD, Garcia LC (2021) Terrestrial invertebrates as bioindicators in restoration ecology: A global bibliometric survey. Ecological Indicators 125: 107458. https://doi.org/10.1016/j.ecolind.2021.107458

Borrow D, Triplehorn C, Johnson N (2000) An introduction to the study of insects. 7a edn., 2000 pp.

Botina GB, Velásquez IA, Bacca T, Castillo FJ, Dias LG (2012) Evaluación de la macrofauna del suelo en solanum tuberosum (solanales: solanaceae) con sistemas de labranza tradicional y mínima. Boletín Científico. Centro de Museos. Museo de Historia Natural 16: 69–77. http://www.scielo.org.co/scielo.php?script=sci_arttext&pid=S0123-30682012000200007&lng=en&nrm=iso&tlng=es [February 13, 2024]

Bottinelli N, Jouquet P, Capowiez Y, Podwojewski P, Grimaldi M, Peng X (2015) Why is the influence of soil macrofauna on soil structure only considered by soil ecologists? Soil & Tillage Research 146: 118–124. https://doi.org/10.1016/j.still.2014.01.007

Bouyoucos G (1936) Directions for Making Mechanical Analysis of Soils by the Hydrometer Method. Soil Science 4(3): 225–228. https://doi.org/10.1097/00010694-193609000-00007

Brandão CR, Silva RR, Delabie JHC (2012) Neotropical Ants (Hymenoptera) Functional Groups: Nutritional and Applied Implications. In: Panizzi A, Parra J (Eds) Insect Bioecology and Nutrition for Integrated Pest Management. CRC Press, Boca Raton, 181–194. https://doi.org/10.1201/b11713-13

Briones MJI (2018) The serendipitous value of soil fauna in ecosystem functioning: The unexplained explained. Frontiers in Environmental Science 6: 421876. https://doi.org/10.3389/fenvs.2018.00149

Brown GG, da Silva E, Thomazini MJ, Niva CC, Decaëns T, Cunha LFN, Nadolny HS, Demetrio WC, Santos A, Ferreira T, Maia LS, Conrado AC, Segalla RF, Ferreira AC, Pasini A, Bartz MLC, Sautter KD, James SW, Baretta D, Antoniolli ZI, Iglesias Briones MJ, Sousa JP, Römbke J, Lavelle P (2018) The role of soil fauna in soil health and delivery of ecosystem services. In: Reicosky D (Ed.) Managing soil health for sustainable agriculture. Burleigh Dodds Science Publishing, London, 197–241. https://doi.org/10.1201/9781351114530

Brown GG, Demetrio WC, Gabriac Q, Pasini A, Korasaki V, Oliveira LJ, dos Santos JCF, Torres E, Galerani PR, Gazziero DLP, Benito NP, Nunes DH, Santos A, Ferreira T, Nadolny HS, Bartz MLC, Maschio W, Dudas RT, Zagatto MRG, Niva CC, Clasen LA, Sautter KD, Froufe LCM, Seoane CES, de Moraes A, James S, Alberton O, Júnior OB, Saraiva O, Garcia A, Oliveira E, César RM, Corrêa-Ferreira BS, Bruz LSM, da Silva E, Cardoso GBX, Lavelle P, Velásquez E, Cremonesi M, Parron LM, Baggio AJ, Neves E, Hungria M, Campos TA, da Silva VL, Reissmann CB, Conrado AC, Bouillet JPD, Gonçalves JLM, Brandani CB, Viani RAG, Paula RR, Laclau JP, Peña-Venegas CP, Peres C, Decaëns T, Pey B, Eisenhauer N, Cooper M, Mathieu J (2024) Soil macrofauna communities in Brazilian land-use systems. Biodiversity Data Journal 12: e115000 12: e115000. https://doi.org/10.3897/BDJ.12.e115000

Brussaard L (1998) Soil fauna, guilds, functional groups and ecosystem processes. Applied Soil Ecology 9(1–3): 123–135. https://doi.org/10.1016/S0929-1393(98)00066-3

Brussaard L, Behan-Pelletier VM, Bignell DE, Brown VK, Didden W, Folgarait P, Fragoso C, Freckman DW, Gupta VVSR, Hattori ST, Hawksworth DL, Klopatek C, Lavelle P, Malloch DW, Rusek J, Söderström B, Tiedje JM, Virginia RA (1997) Biodiversity and ecosystem functioning in soil. Ambio 26: 563–570.

Brussaard L, de Ruiter PC, Brown GG (2007) Soil biodiversity for agricultural sustainability. Agriculture, Ecosystems & Environment 121(3): 233–244. https://doi.org/10.1016/j.agee.2006.12.013

Cameron E, Martins I, Lavelle P, Mathieu J, Tedersoo L, Gottschall F, Guerra CA, Hines J, Patoine G, Siebert J, Winter M, Cesarz S, Delgado-Baquerizo M, Ferlian O, Fierer N, Kreft H, Lovejoy L, Montanarella L, Orgiazzi A, Pereira H, Phillips HRP, Settele J, Wall DH, Eisenhauer N (2018) Global gaps in soil biodiversity data. Nature Ecology & Evolution 2(7): 1042–1043. https://doi.org/10.1038/s41559-018-0573-8

Carneiro MAC, de Souza ED, dos Reis EF, Pereira HS, de Azevedo WR (2009) Atributos físicos, químicos e biológicos de solo de cerrado sob diferentes sistemas de uso e manejo. Revista Brasileira de Ciência do Solo 33(1): 147–157. https://doi.org/10.1590/S0100-06832009000100016

Caron TMF, Chuma VJUR, Sandi AA, Norris D (2021) Big trees drive forest structure patterns across a lowland Amazon regrowth gradient. Scientific Reports 2021 11:1: 1–12. https://doi.org/10.1038/s41598-021-83030-5

Carrijo TF, Pontes-Nogueira M, Santos RG, Morales AC, Cancello EM, Scheffrahn RH (2020) New World Heterotermes (Isoptera, Rhinotermitidae): Molecular phylogeny, biogeography and description of a new species. Systematic Entomology 45(3): 527–539. https://doi.org/10.1111/syen.12412

Carrijo TF, Castro D, Wang M, Constantini JP, Bourguignon T, Cancello EM, Roisin Y, Scheffrahn RH (2023) Diminishing the taxonomic gap in the neotropical soldierless termites: descriptions of four new genera and a new Anoplotermes species (Isoptera,

Termitidae, Apicotermitinae). ZooKeys 1167: 317–352. https://doi.org/10.3897/zookeys.1167.100001

Casari SA, Melo GAR de, Carvalho CJB de, Casari SA, Constantino R (2024) Insetos do Brasil: Diversidade e Taxonomia. https://doi.org/10.61818/56330464

Casas C, Pineda N, Monroy D, Realpe E, Noriega JA (2021) Variación estacional de la biomasa de un ensamble de escarabajos coprófagos (Coleoptera: Scarabaeinae) en un pastizal altoandino. Acta Biologica Colombiana 26(3): 318–326. https://doi.org/10.15446/abc.v26n3.84603

Castro D, Scheffrahn RH (2019) A new species of *Acorhinotermes* Emerson, 1949 (Blattodea, Isoptera, Rhinotermitidae) from Colombia, with a key to Neotropical Rhinotermitinae species based on minor soldiers. ZooKeys 891: 61–70. https://doi.org/10.3897/zookeys.891.37523

Castro D, Fernández F, Meneses AD, Tocora MC, Sanchez S, Peña-Venegas CP (2018) A preliminary checklist of soil ants (Hymenoptera: Formicidae) of Colombian Amazon. Biodiversity Data Journal 6: e29278. https://doi.org/10.3897/BDJ.6.e29278

Castro D, Carrijo TF, Serna FJ, Peña-Venegas CP (2021) Can Rubber Crop Systems Recover Termite Diversity in Previously Degraded Pastures in the Colombian Amazon Region? Neotropical Entomology 50(6): 899–911. https://doi.org/10.1007/s13744-021-00905-y

Cerón P, Montenegro S, Noguera E (2008) Macrofauna En Suelos De Bosque Y Pajonal De La Reserva Natural Pueblo Viejo, Nariño, Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 32(125): 447–453. https://doi.org/10.18257/raccefyn.32(125).2008.2311

Chao A, Chiu C-H (2016) Species Richness: Estimation and Comparison. Wiley StatsRef: Statistics Reference Online, 1–26. https://doi.org/10.1002/9781118445112.stat03432.pub2

Cherubin MR, Chavarro-Bermeo JP, Silva-Olaya AM (2019) Agroforestry systems improve soil physical quality in northwestern Colombian Amazon. Agroforestry Systems 93(5): 1741–1753. https://doi.org/10.1007/s10457-018-0282-y

Cole RJ, Holl KD, Zahawi RA, Wickey P, Townsend AR (2016) Leaf litter arthropod responses to tropical forest restoration. Ecology and Evolution 6(15): 5158–5168. https://doi.org/10.1002/ece3.2220

Cole RJ, Selmants P, Khan S, Chazdon R (2019) Litter dynamics recover faster than arthropod biodiversity during tropical forest succession. Biotropica 52(1): 22–33. https://doi.org/10.1111/btp.12740

Conrado AC, Demetrio WC, Stanton DWG, Bartz MLC, James SW, Santos A, da Silva E, Ferreira T, Acioli ANS, Ferreira AC, Maia LS, Silva TAC, Lavelle P, Velasquez E, Tapia-Coral SC, Muniz AW, Segalla RF, Decaëns T, Nadolny HS, Peña-Venegas CP, Pasini A, de Oliveira Júnior RC, Kille P, Brown GG, Cunha L (2023) Amazonian earthworm biodiversity is heavily impacted by ancient and recent human disturbance. The Science of the Total Environment 895: 165087. https://doi.org/10.1016/j.scitotenv.2023.165087

Constantino R (2002) An illustrated key to Neotropical termite genera (Insecta: Isoptera) based primarily on soldiers. Zootaxa 40(1): 1–40. https://doi.org/10.11646/zootaxa.67.1.1

Corwin DL, Yemoto K (2017) Salinity: electrical conductivity and total dissolved solids. Methods of Soil Analysis. Soil Science Society of America, Madison, WI, 16 pp. https://doi.org/10.2136/msa2015.0039

Cromack K, Sollins P, Todd RL, Crossley DA, Fender WM, Fogel R, Todd AW (1977) Soil Microorganism—Arthropod Interactions: Fungi as Major Calcium and Sodium Sources. In: Mattson W (Ed.) The Role of Arthropods in Forest Ecosystems. Pro-

ceedings in Life Sciences. Springer, Berlin, 78–84. https://doi.org/10.1007/978-3-642-88448-1_9

Dahlsjö CAL, Parr CL, Malhi Y, Rahman H, Meir P, Jones DT, Eggleton Journal P, Eggleton P (2014) First comparison of quantitative estimates of termite biomass and abundance reveals strong intercontinental differences. Journal of Tropical Ecology 30(2): 143–152. https://doi.org/10.1017/S0266467413000898

Dambros CS, Morais JW, Vasconcellos A, Souza JLP, Franklin E, Gotelli NJ (2016) Association of Ant Predators and Edaphic Conditions with Termite Diversity in an Amazonian Rain Forest. Biotropica 48(2): 237–245. https://doi.org/10.1111/btp.12270

De Carvalho Balieiro F, Pereira MG, Alves BJR, De Resende AS, Franco AA (2008) Soil carbon and nitrogen in pasture soil reforested with Eucalyptus and guachapele. Revista Brasileira de Ciência do Solo 32(3): 1253–1260. https://doi.org/10.1590/S0100-06832008000300033

De Farias PM, Hernández MIM (2017) Dung Beetles Associated with Agroecosystems of Southern Brazil: Relationship with Soil Properties. Revista Brasileira de Ciência do Solo 41(0): 160248. https://doi.org/10.1590/18069657rbcs20160248

de Paula RC, de Moraes Lima Silveira R, da Rocha MM, Izzo TJ (2016) The restoration of termite diversity in different reforestated forests. Agroforestry Systems 90(3): 395–404. https://doi.org/10.1007/s10457-015-9862-2

de Souza TAF, Freitas H (2018) Long-Term Effects of Fertilization on Soil Organism Diversity. In: Gaba S, Smith B, Lichtfouse E (Eds) Sustainable Agriculture Reviews, vol. 28. Springer, 211–247. https://doi.org/10.1007/978-3-319-90309-5_7

de Vasconcelos WLF, Rodrigues D de M, Silva ROC, Alfaia SS (2020) Diversity and abundance of soil macrofauna in three land use systems in Eastern Amazonia. Revista Brasileira de Ciência do Solo 44: 1–16. https://doi.org/10.36783/18069657rbcs20190136

Decaëns T, Jiménez JJ, Gioia C, Measey GJ, Lavelle P (2006) The values of soil animals for conservation biology. European Journal of Soil Biology 42: S23–S38. https://doi.org/10.1016/j.ejsobi.2006.07.001

Demetrio WC, Conrado AC, Acioli ANS, Casadei Ferreira A, Bartz MLC, James SW, da Silva E, Maia LS, Martins GC, Macedo RS, Stanton DWG, Lavelle P, Velasquez E, Zangerlé A, Barbosa R, Tapia-Coral SC, Muniz AW, Santos A, Ferreira T, Segalla RF, Decaëns T, Nadolny HS, Peña-Venegas CP, Maia CMBF, Pasini A, Mota AF, Taube Júnior PS, Silva TAC, Rebellato L, de Oliveira Júnior RC, Neves EG, Lima HP, Feitosa RM, Vidal Torrado P, McKey D, Clement CR, Shock MP, Teixeira WG, Motta ACV, Melo VF, Dieckow J, Garrastazu MC, Chubatsu LS, Kille P, Brown GG, Cunha L (2021) A"Dirty" Footprint: Macroinvertebrate diversity in Amazonian Anthropic Soils. Global Change Biology 00(19): 1–17. https://doi.org/10.1111/gcb.15752

Diehl E, Sanhudo CED, Diehl-Fleig E (2004) Ground-dwelling ant fauna of sites with high levels of copper. Brazilian Journal of Biology 64(1): 33–39. https://doi.org/10.1590/S1519-69842004000100005

Domínguez J, Bohlen PJ, Parmelee RW (2004) Earthworms Increase Nitrogen Leaching to Greater Soil Depths in Row Crop Agroecosystems. Ecosystems 2004 7:6 7: 672–685. https://doi.org/10.1007/s10021-004-0150-7

Donoso DA, Johnston MK, Kaspari M (2010) Trees as templates for tropical litter arthropod diversity. Oecologia 164(1): 201–211. https://doi.org/10.1007/s00442-010-1607-3

Donovan SE, Eggleton P, Bignell DE (2001) Gut content analysis and a new feeding group classification of termites. Ecological Entomology 26(4): 356–366. https://doi.org/10.1046/j.1365-2311.2001.00342.x

Dray S, Dufour A-B, Thioulouse J (2020) ade4: analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences. R package version 1.7-16.

Duran-Bautista EH, Muñoz Y, Galindo JD, Ortiz T, Bermúdez M (2020) Soil physical quality and relationship to changes in termite community in northwestern Colombian Amazon. Frontiers in Ecology and Evolution 8: 598134. https://doi.org/10.3389/fevo.2020.598134

Duran-Bautista EH, Angel-Sanchez YK, Bermúdez MF, Suárez JC (2023) Agroforestry systems generate changes in soil macrofauna and soil physical quality relationship in the northwestern Colombian Amazon. Agroforestry Systems 97(5): 927–938. https://doi.org/10.1007/s10457-023-00838-y

Evangelista DA, Russell G, Russell KN, Bourne G, Ware JL (2017) Evidence that dispersal barriers influence blaberoid cockroach assemblages in a neotropical savanna–forest matrix. Insect Conservation and Diversity 10(5): 425–438. https://doi.org/10.1111/icad.12246

Evans TA, Dawes TZ, Ward PR, Lo N (2011) Ants and termites increase crop yield in a dry climate. Nature Communications 2(1): 262–267. https://doi.org/10.1038/ncomms1257

Fallah M, Farzam M, Hosseini V, Moravej G, Eldridge DJ (2017) Termite effects on soils and plants are generally consistent along a gradient in livestock grazing. Arid Land Research and Management 31(2): 159–168. https://doi.org/10.1080/15324982.2017.1288177

FAO, ITPS, GSBI, CBD, EC (2020) State of knowledge of soil biodiversity - Status, challenges and potentialities. Food and agriculture organization of the united nations, Rome, Italia, 583 pp. https://doi.org/10.4060/cb1928en

FAO (2021) Global Forest Resources Assessments. FRA 2020 Remote Sensing Survey. https://doi.org/10.4060/cb9970en

Farrell KA, Harpole WS, Stein C, Suding KN, Borer ET (2015) Grassland Arthropods Are Controlled by Direct and Indirect Interactions with Cattle but Are Largely Unaffected by Plant Provenance. PLoS ONE 10(7): e0129823. https://doi.org/10.1371/journal.pone.0129823

Feldpausch TR, Riha SJ, Fernandes ECM, Wandelli EV (2005) Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia. Earth Interactions 9(6): 1–22. https://doi.org/10.1175/EI140.1

Fernández F, Guerrero Flórez RJ, Delsinne T (2019) Hormigas de Colombia Hormigas de Colombia. Universidad Nacional de Colombia, Bogotá D.C., 1200 pp. https://doi.org/10.21676/9789587837650

Fittkau EJ, Klinge H (1973) On Biomass and Trophic Structure of the Central Amazonian Rain Forest Ecosystem. Biotropica 5(1): 2. https://doi.org/10.2307/2989676

Forstall-Sosa KS, de Souza TAF, de Oliveira Lucena E, da Silva SIA, Ferreira JTA, do Nascimento Silva T, Santos D, Niemeyer JC (2021) Soil macroarthropod community and soil biological quality index in a green manure farming system of the Brazilian semi-arid. Biologia 76: 907–917. https://doi.org/10.2478/s11756-020-00602-y

Franco ALC, Sobral BW, Silva ALC, Wall DH (2019) Amazonian deforestation and soil biodiversity. Conservation Biology 33(3): 590–600. https://doi.org/10.1111/cobi.13234

Frouz J (2024) The Role of Earthworms in Soil Formation. In: Kooch Y, Kuzyakov Y (Eds) Earthworms and Ecological Processes. Springer Cham, Switzerland, 323–339. https://doi.org/10.1007/978-3-031-64510-5_11

Gerlach J, Samways M, Pryke J (2013) Terrestrial invertebrates as bioindicators: An overview of available taxonomic groups. Journal of Insect Conservation 17(4): 831–850. https://doi.org/10.1007/s10841-013-9565-9

Gongalsky KB (2021) Soil macrofauna: Study problems and perspectives. Soil Biology & Biochemistry 159: 108281. https://doi.org/10.1016/j.soilbio.2021.108281

Gonzalez G, Zou X (1999) Earthworm influence on N availability and the growth of Cecropia schreberiana in tropical pasture and forest soils | Treesearch. Pedobiologia 43: 824–829. https://doi.org/10.1016/S0031-4056(24)00618-8

González-González A, Clerici N, Quesada B (2021) Growing mining contribution to Colombian deforestation. Environmental Research Letters 16(6): 064046. https://doi.org/10.1088/1748-9326/abfcf8

Griffiths HM, Ashton LA, Evans TA, Parr CL, Eggleton P (2019) Termites can decompose more than half of deadwood in tropical rainforest. Current Biology 29(4): R118–R119. https://doi.org/10.1016/j.cub.2019.01.012

Guerra CA, Heintz-Buschart A, Sikorski J, Chatzinotas A, Guerrero-Ramírez N, Cesarz S, Beaumelle L, Rillig MC, Maestre FT, Delgado-Baquerizo M, Buscot F, Overmann J, Patoine G, Phillips HRP, Winter M, Wubet T, Küsel K, Bardgett RD, Cameron EK, Cowan D, Grebenc T, Marín C, Orgiazzi A, Singh BK, Wall DH, Eisenhauer N (2020) Blind spots in global soil biodiversity and ecosystem function research. Nature Communications 11:1: 1–13. https://doi.org/10.1038/s41467-020-17688-2

Guimarães N, Akio A, Arroyo R, de Souza A, de Carvalho E, da Silva R (2020) Edaphic invertebrate macrofauna associated with cassava crop in different soil coverages. Australian Journal of Crop Science 14(12): 1835–2707. https://doi.org/10.21475/ajcs.20.14.12.2822

Hill GM, Shannon MC (2019) Copper and Zinc Nutritional Issues for Agricultural Animal Production. Biological Trace Element Research 188(1): 148–159. https://doi.org/10.1007/s12011-018-1578-5

Höffer H, Hanagarth W, Garcia M, Martius C, Franklin E, Beck L (2001) Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. European Journal of Soil Biology 37(4): 229–235. https://doi.org/10.1016/S1164-5563(01)01089-5

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. Biometrical Journal. Biometrische Zeitschrift 50(3): 346–363. https://doi.org/10.1002/bimj.200810425

Hothorn T, Brezt F, Westfall P, Heiberger R, Schuetzenmeister A, Scheibe S (2023) Simultaneous Inference in General Parametric Models - Package 'multcomp' Version 1.4-25. http://multcomp.r-forge.r-project.org

Hsieh TC, Ma KH, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7(12): 1451–1456. https://doi.org/10.1111/2041-210X.12613

Husson F, Josse J, Le S, Maintainer JM (2020) Package "FactoMineR" Title Multivariate Exploratory Data Analysis and Data Mining. Version 2.3. http://factominer.free.fr

IGAC (2014) Estudio General de Suelos y Zonificación de Tierras Departamento de Caquetá, Escala 1:100,000. Imprenta nacional de Colombia, Bogotá D.C., 410 pp.

ISO (2011) ISO 23611-5 Soil quality: Sampling of soil invertebrates. Part 5: Sampling and extraction of soil macro-invertebrates, 12 pp.

Jouquet P, Traoré S, Choosai C, Hartmann C, Bignell D (2011) Influence of termites on ecosystem functioning. Ecosystem services provided by termites. European Journal of Soil Biology 47(4): 215–222. https://doi.org/10.1016/j.ejsobi.2011.05.005

Jouquet P, Blanchart E, Capowiez Y (2014) Utilization of earthworms and termites for the restoration of ecosystem functioning. Applied Soil Ecology 73: 34–40. https://doi.org/10.1016/j.apsoil.2013.08.004

Kalaiyarasi M, Saravanan S, Balaji R, Karthi S, Rao DSNM, Sireesha DNV (2023) Estimation of Deforestation Rate and Forest Land Use Land Cover Change Detection.

Proceedings of the International Conference on Artificial Intelligence and Knowledge Discovery in Concurrent Engineering, ICECONF 2023. https://doi.org/10.1109/ICECONF57129.2023.10083928

Kassambara A, Mundt F (2020) factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7.

Klink R, van, Plas F, van der Noordwijk CGE (2015) Effects of large herbivores on grassland arthropod diversity. Biological Reviews of the Cambridge Philosophical Society 90(2): 347–366. https://doi.org/10.1111/brv.12113

Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, Lindborg R, Öckinger E, Pärtel M, Pino J, Pöyry J, Raatikainen KM, Sang A, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13(5): 597–605. https://doi.org/10.1111/j.1461-0248.2010.01457.x

Krishna K, Araujo RL (1968) A revision of the Neotropical termite genus *Neocapritermes* (Isoptera, Termitidae, Termitinae). Bulletin of the American Museum of Natural History 138: 83–130.

Lamarre GPA, Erault BH, Fine PVA, Vedel V, Lupoli R, Mesones I, Baraloto C (2016) Taxonomic and functional composition of arthropod assemblages across contrasting Amazonian forests. Journal of Animal Ecology 85(1): 227–239. https://doi.org/10.1111/1365-2656.12445

Lapola DM, Pinho P, Barlow J, Aragão LEOC, Berenguer E, Carmenta R, Liddy HM, Seixas H, Silva CVJ, Silva CHL, Alencar AAC, Anderson LO, Armenteras D, Brovkin V, Calders K, Chambers J, Chini L, Costa MH, Faria BL, Fearnside PM, Ferreira J, Gatti L, Gutierrez-Velez VH, Han Z, Hibbard K, Koven C, Lawrence P, Pongratz J, Portela BTT, Rounsevell M, Ruane AC, Schaldach R, da Silva SS, von Randow C, Walker WS (2023) The drivers and impacts of Amazon forest degradation. Science 379(6630): eabp8622. https://doi.org/10.1126/science.abp8622

Lavelle P, Dangerfield M, Fragoso C, Eschenbrenner V, Lopez-Hernandez D, Pashanasi B, Brussaard L (1994) The relationship between soil macrofauna and tropical soil fertility, 137–169.

Lavelle P, Mathieu J, Spain A, Brown G, Fragoso C, Lapied E, De Aquino A, Barois I, Barrios E, Barros ME, Bedano JC, Blanchart E, Caulfield M, Chagueza Y, Dai J, Decaëns T, Dominguez A, Dominguez Y, Feijoo A, Folgarait P, Fonte SJ, Gorosito N, Huerta E, Jimenez JJ, Kelly C, Loranger G, Marchão R, Marichal R, Praxedes C, Rodriguez L, Rousseau G, Rousseau L, Ruiz N, Sanabria C, Suarez JC, Tondoh JE, De Valença A, Vanek SJ, Vasquez J, Velasquez E, Webster E, Zhang C (2022) Soil macroinvertebrate communities: A world-wide assessment. Global Ecology and Biogeography 31(7): 1261–1276. https://doi.org/10.1111/geb.13492

Lê S, Josse J, Husson F (2008) FactoMineR: An R package for multivariate analysis. Journal of Statistical Software 25(1): 1–18. https://doi.org/10.18637/jss.v025.i01

Lepage M, Abbadie L, Josens G, Lavelle P (2006) Lamto. Ecological Studies, Vol 179. In: Abbadie L, Gignoux J, Le Roux X, Lepage M (Eds) Role of Soil Fauna in Nitrogen Cycling. Springer, New York, 299–311. https://doi.org/10.1007/978-0-387-33857-6_16

Lima SS, Pereira MG, Pereira RN, Pontes RM, Rossi CQ (2018) Termite mounds effects on soil properties in the atlantic forest biome. Revista Brasileira de Ciência do Solo 42(0): e0160564. https://doi.org/10.1590/18069657rbcs20160564

Liu J, Wilson M, Hu G, Liu J, Wu J, Yu M (2018) How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? Landscape Ecology 33: 341–352. https://doi.org/10.1007/s10980-018-0620-5

Lüdecke D (2024) sjPlot. Data Visualization for Statistics in Social Science, 107 pp. https://doi.org/10.32614/CRAN.package.sjPlot

Marchão RL, Lavelle P, Leonide C, Balbino C, Vilela L, Becquer T (2009) Pesq. agropec. bras Soil macrofauna under integrated crop-livestock systems in a Brazilian Cerrado Ferralsol. https://doi.org/10.1590/S0100-204X2009000800033

Marichal R, Grimaldi M, Feijoo MA, Oszwald J, Praxedes C, Ruiz Cobo DH, del Pilar Hurtado M, Desjardins T, da Silva ML Junior, da Silva Costa LG, Miranda IS, Delgado Oliveira MN, Brown GG, Tsélouiko S, Martins MB, Decaëns T, Velasquez E, Lavelle P (2014) Soil macroinvertebrate communities and ecosystem services in deforested landscapes of Amazonia. Applied Soil Ecology 83: 177–185. https://doi.org/10.1016/j.apsoil.2014.05.006

Mathieu J, Antunes AC, Barot S, Asato AEB, Bartz MLC, Brown GG, Calderon-Sanou I, Decaëns T, Fonte SJ, Ganault P, Gauzens B, Gongalsky KB, Guerra CA, Hengl T, Lavelle P, Marichal R, Mehring H, Peña-Venegas CP, Castro D, Potapov A, Thébault E, Thuiller W, Witjes M, Zhang C, Eisenhauer N (2022) sOilFauna - a global synthesis effort on the drivers of soil macrofauna communities and functioning. Soil Organisms 94: 111–126. https://doi.org/10.25674/SO94ISS2ID282

Meloni F, Varanda EM (2015) Litter and soil arthropod colonization in reforested semi-deciduous seasonal Atlantic forests. Restoration Ecology 23(5): 690–697. https://doi.org/10.1111/rec.12236

Menta C (2012) Soil Fauna Diversity - Function, Soil Degradation, Biological Indices, Soil Restoration. Biodiversity Conservation and Utilization in a Diverse World. InTech. https://doi.org/10.5772/51091

Mesquita R de CG, Massoca PES, Jakovac CC, Bentos TV, Williamson GB (2015) Amazon Rain Forest Succession: Stochasticity or Land-Use Legacy? Bioscience 65(9): 849–861. https://doi.org/10.1093/biosci/biv108

Moradi J, John K, Vicentini F, Veselá H, Vicena J, Ardestani MM, Frouz J (2020) Vertical distribution of soil fauna and microbial community under two contrasting post mining chronosequences: Sites reclaimed by alder plantation and unreclaimed regrowth. Global Ecology and Conservation 23: e01165. https://doi.org/10.1016/j.gecco.2020.e01165

Moran MD, Hurd LE (1997) A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. Oecologia 113(1): 126–132. https://doi.org/10.1007/s004420050360

Murad CA, Pearse J (2018) Landsat study of deforestation in the Amazon region of Colombia: Departments of Caquetá and Putumayo. Remote Sensing Applications: Society and Environment 11: 161–171. https://doi.org/10.1016/j.rsase.2018.07.003

Ndiaye D, Lepage M, Sall CE, Brauman A (2004) Nitrogen transformations associated with termite biogenic structures in a dry savanna ecosystem. Plant and Soil 265(1–2): 189–196. https://doi.org/10.1007/s11104-005-0892-9

Orgiazzi A, Singh B, Wall D, Barrios E, Kandeler E, Moreira F, De Deyn G, Chotte J, Six J, Hedlund K, Briones M, Miko L, Johnson N, Ramirez K, Fierer N, Kaneko N, Lavelle P, Eggleton P, Lemanceau P, Bardgett R, Jeffery S, Fraser T, Behan Pelletier V, Van Der Putten W, Montanarella L, Jones A (2016) Global Soil Biodiversity Atlas. Publications Office of the European Union, Luxembourg, 176 pp.

Paquin P, Coderre D (2017) International Association for Ecology Changes in Soil Macroarthropod Communities in Relation to Forest Maturation through Three Successional Stages in the Canadian Boreal Forest Published by : Springer in cooperation with International Association for Eco. Oecologia 112(1): 104–111. https://doi.org/10.1007/s004420050289

Pauli N, Barrios E, Conacher AJ, Oberthür T (2011) Soil macrofauna in agricultural landscapes dominated by the Quesungual Slash-and-Mulch Agroforestry System, western Honduras. Applied Soil Ecology 47(2): 119–132. https://doi.org/10.1016/j.apsoil.2010.11.005

Pendrill F, Persson UM (2017) Combining global land cover datasets to quantify agricultural expansion into forests in Latin America: Limitations and challenges. PLoS ONE 12: e0181202. https://doi.org/10.1371/journal.pone.0181202

Phillips HRP, Bach EM, Bartz MLC, Bennett JM, Beugnon R, Briones MJI, Brown GG, Ferlian O, Gongalsky KB, Guerra CA, König-Ries B, Krebs JJ, Orgiazzi A, Ramirez KS, Russell DJ, Schwarz B, Wall DH, Brose U, Decaëns T, Lavelle P, Loreau M, Mathieu J, Mulder C, van der Putten WH, Rillig MC, Thakur MP, de Vries FT, Wardle DA, Ammer C, Ammer S, Arai M, Ayuke FO, Baker GH, Baretta D, Barkusky D, Beauséjour R, Bedano JC, Birkhofer K, Blanchart E, Blossey B, Bolger T, Bradley RL, Brossard M, Burtis JC, Capowiez Y, Cavagnaro TR, Choi A, Clause J, Cluzeau D, Coors A, Crotty FV, Crumsey JM, Dávalos A, Cosín DJD, Dobson AM, Domínguez A, Duhour AE, van Eekeren N, Emmerling C, Falco LB, Fernández R, Fonte SJ, Fragoso C, Franco ALC, Fusilero A, Geraskina AP, Gholami S, González G, Gundale MJ, López MG, Hackenberger BK, Hackenberger DK, Hernández LM, Hirth JR, Hishi T, Holdsworth AR, Holmstrup M, Hopfensperger KN, Lwanga EH, Huhta V, Hurisso TT, Iannone BV III, Iordache M, Irmler U, Ivask M, Jesús JB, Johnson-Maynard JL, Joschko M, Kaneko N, Kanianska R, Keith AM, Kernecker ML, Koné AW, Kooch Y, Kukkonen ST, Lalthanzara H, Lammel DR, Lebedev IM, Le Cadre E, Lincoln NK, López-Hernández D, Loss SR, Marichal R, Matula R, Minamiya Y, Moos JH, Moreno G, Morón-Ríos A, Motohiro H, Muys B, Neirynck J, Norgrove L, Novo M, Nuutinen V, Nuzzo V, Mujeeb Rahman P, Pansu J, Paudel S, Pérès G, Pérez-Camacho L, Ponge JF, Prietzel J, Rapoport IB, Rashid MI, Rebollo S, Rodríguez M, Roth AM, Rousseau GX, Rozen A, Sayad E, van Schaik L, Scharenbroch B, Schirrmann M, Schmidt O, Schröder B, Seeber J, Shashkov MP, Singh J, Smith SM, Steinwandter M, Szlavecz K, Talavera JA, Trigo D, Tsukamoto J, Uribe-López S, de Valença AW, Virto I, Wackett AA, Warren MW, Webster ER, Wehr NH, Whalen JK, Wironen MB, Wolters V, Wu P, Zenkova IV, Zhang W, Cameron EK, Eisenhauer N (2021) Global data on earthworm abundance, biomass, diversity and corresponding environmental properties. Scientific Data 8(1): 136. https://doi.org/10.1038/s41597-021-00912-z

Pollierer MM, Klarner B, Ott D, Digel C, Ehnes RB, Eitzinger B, Erdmann G, Brose U, Maraun M, Scheu S (2021) Diversity and functional structure of soil animal communities suggest soil animal food webs to be buffered against changes in forest land use. Oecologia 1(1): 3. https://doi.org/10.1007/s00442-021-04910-1

Qu X, Li X, Bardgett RD, Kuzyakov Y, Revillini D, Sonne C, Xia C, Ruan H, Liu Y, Cao F, Reich PB, Delgado-Baquerizo M (2024) Deforestation impacts soil biodiversity and ecosystem services worldwide. Proceedings of the National Academy of Sciences of the United States of America 121(13): e2318475121. https://doi.org/10.1073/pnas.2318475121

R Core Team (2023) R: A language and environment for statistical computing. https://www.r-project.org/

Reddell J (1983) A Checklist and Bibliography of the Japygoidea (Insecta: Diplura) of North America, Central America, and the West Indies. Pearce-Sellards Series. Texas Memorial Museum, The University of Texas at Austin: 39. http://hdl.handle.net/2152/29904

Roberts RJ, Morton R (1985) Biomass of Larval Scarabaeidae (Coleoptera) in Relation to Grazing Pressures in Temperate, Sown Pastures. Journal of Applied Ecology 22(3): 863. https://doi.org/10.2307/2403235

Rocha MM, Cancello EM (2007) Estudo taxonômico de *Cylindrotermes* Holmegren (Isoptera, Termitidae Termitinae). Papéis Avulsos de Zoologia da Universidade de São Paulo 47: 137–152. https://doi.org/10.1590/S0031-10492007001000001

Rocha MM, Cancello EM (2022) Updated taxonomy of Syntermitinae (Blattodea: Isoptera, Termitidae), with the description of three new genera. Zootaxa 5138(4): 445–463. https://doi.org/10.11646/zootaxa.5138.4.6

Rodríguez L, Suárez Salazar JC, Casanoves F, Ngo Bieng MA (2021a) Cacao agroforestry systems improve soil fertility: Comparison of soil properties between forest, cacao agroforestry systems, and pasture in the Colombian Amazon. Agriculture, Ecosystems & Environment 314: 107349. https://doi.org/10.1016/j.agee.2021.107349

Rodríguez L, Suárez JC, Pulleman M, Guaca L, Rico A, Romero M, Quintero M, Lavelle P (2021b) Agroforestry systems in the Colombian Amazon improve the provision of soil ecosystem services. Applied Soil Ecology 164: 103933. https://doi.org/10.1016/j.apsoil.2021.103933

Rodríguez-León CH, Peña-Venegas CP, Sterling A, Castro D, Mahecha-Virguez LK, Virguez-Díaz YR, Silva-Olaya AM, Guerrero GG, Méndez A (2021) Soil Quality Restoration during the Natural Succession of Abandoned Cattle Pastures in Deforested Landscapes in the Colombian Amazon. Agronomy 2021 11: 2484. https://doi.org/10.3390/agronomy11122484

Rousseau GX, Silva PR dos S, Celentano D, de Carvalho CJR (2014) Macrofauna do solo em uma cronosequência de capoeiras, florestas e pastos no Centro de Endemismo Belém, Amazônia Oriental. Acta Amazonica 44(4): 499–512. https://doi.org/10.1590/1809-4392201303245

Ruiz N, Lavelle P, Jiménez J (2008) Soil macrofauna: field manual - technical level. FAO, Rome, Italia, 113 pp.

Sanabria C, Dubs F, Lavelle P, Fonte SJ, Barot S (2016) Influence of regions, land uses and soil properties on termite and ant communities in agricultural landscapes of the Colombian Llanos. European Journal of Soil Biology 74: 81–92. https://doi.org/10.1016/j.ejsobi.2016.03.008

Sanders D, van Veen FJF (2011) Ecosystem engineering and predation: The multi-trophic impact of two ant species. Journal of Animal Ecology 80(3): 569–576. https://doi.org/10.1111/j.1365-2656.2010.01796.x

Schaefer C, Marins A, Redende G, De Souza OFF, Nunes J (2016) Termite role in soil nutrient cycling in ironstone rupestrian grasslands (Canga) in Carajás, Brazilian Amazonia. In: Fernandes G (Ed.) Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer, 1–567. https://doi.org/10.1007/978-3-319-29808-5

Schroth G, Garcia E, Griscom BW, Teixeira WG, Barros LP (2015) Commodity production as restoration driver in the Brazilian Amazon? Pasture re-agro-forestation with cocoa (Theobroma cacao) in southern Pará. Sustainability Science 11: 277–293. https://doi.org/10.1007/s11625-015-0330-8

Serra RT, Santos CD, Rousseau GX, Triana SP, Muñoz Gutiérrez JA, Burgos Guerrero JE (2021) Fast recovery of soil macrofauna in regenerating forests of the Amazon. Journal of Animal Ecology 00(9): 1–15. https://doi.org/10.1111/1365-2656.13506

Sharrow SH (2007) Soil compaction by grazing livestock in silvopastures as evidenced by changes in soil physical properties. Agroforestry Systems 71(3): 215–223. https://doi.org/10.1007/s10457-007-9083-4

Snyder BA, Hendrix PF (2008) Current and Potential Roles of Soil Macroinvertebrates (Earthworms, Millipedes, and Isopods) in Ecological Restoration. Restoration Ecology 16(4): 629–636. https://doi.org/10.1111/j.1526-100X.2008.00484.x

Sofo A, Mininni AN, Ricciuti P (2020) Soil Macrofauna: A key Factor for Increasing Soil Fertility and Promoting Sustainable Soil Use in Fruit Orchard Agrosystems. Agronomy 2020 10: 456. https://doi.org/10.3390/agronomy10040456

Solar RR de C, Barlow J, Andersen AN, Schoereder JH, Berenguer E, Ferreira JN, Gardner TA (2016) Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. Biological Conservation 197: 98–107. https://doi.org/10.1016/j.biocon.2016.03.005

Souty-Grosset C, Faberi A (2018) Effect of agricultural practices on terrestrial isopods: A review. ZooKeys 63: 63–96. https://doi.org/10.3897/zookeys.801.24680

Suárez LR, Josa YTP, Samboni EJA, Cifuentes KDL, Bautista EHD, Salazar JCS (2018) Soil macrofauna under different land uses in the Colombian Amazon. Pesquisa Agropecuária Brasileira 53(12): 1383–1391. https://doi.org/10.1590/s0100-204x2018001200011

Tulande-M E, Barrera-Cataño J, Alonso-Malaver C, Morantes-Ariza C, Basto S (2018) Soil macrofauna in areas with different ages after Pinus patula clearcutting. Universitas Scientiarum 23(3): 383–417. https://doi.org/10.11144/Javeriana.SC23-3.smia

Tuma J, Eggleton P, Fayle TM (2020) Ant-termite interactions: An important but under-explored ecological linkage. Biological Reviews of the Cambridge Philosophical Society 95(3): 555–572. https://doi.org/10.1111/brv.12577

Uhl C, Buschbacher R, Serrao EAS (1988) Abandoned Pastures in Eastern Amazonia. I. Patterns of Plant Succession. Journal of Ecology 76(3): 663. https://doi.org/10.2307/2260566

Van Zwieten L, Rust J, Kingston T, Merrington G, Morris S (2004) Influence of copper fungicide residues on occurrence of earthworms in avocado orchard soils. The Science of the Total Environment 329(1–3): 29–41. https://doi.org/10.1016/j.scitotenv.2004.02.014

Vazquez E, Teutscherova N, Lojka B, Arango J, Pulleman M (2020) Pasture diversification affects soil macrofauna and soil biophysical properties in tropical (silvo) pastoral systems. Agriculture, Ecosystems & Environment 302: 107083. https://doi.org/10.1016/j.agee.2020.107083

Veldkamp E, Schmidt M, Powers JS, Corre MD (2020) Deforestation and reforestation impacts on soils in the tropics. Nature Reviews Earth & Environment 2020 1: 590–605. https://doi.org/10.1038/s43017-020-0091-5

Vieira DLM, Rodrigues SB, Jakovac CC, Rocha GPE da, Reis F, Borges A (2021) Active Restoration Initiates High Quality Forest Succession in a Deforested Landscape in Amazonia. Forests 2021, 12: 1022. https://doi.org/10.3390/f12081022

Walkley A, Black IA (1934) An examination of the degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Science 37(1): 29–38. https://doi.org/10.1097/00010694-193401000-00003

Wilkie KTR, Mertl AL, Traniello JFA (2010) Species Diversity and Distribution Patterns of the Ants of Amazonian Ecuador. PLoS ONE 5(10): e13146. https://doi.org/10.1371/journal.pone.0013146

Supplementary material 1

Locations where macroarthropods were collected for this study

Authors: Daniel Castro, Clara P. Peña-Venegas, Carlos H. Rodríguez-León, Ervin H. Duran-Bautista, Armando Sterling

Data type: docx

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Link: https://doi.org/10.3897/natureconservation.58.136370.suppl1

Supplementary material 2

Composition of soil macroarthropod morphospecies

Authors: Daniel Castro, Clara P. Peña-Venegas, Carlos H. Rodríguez-León, Ervin H. Duran-Bautista, Armando Sterling

Data type: docx

Explanation note: Composition of soil macroarthropod morphospecies from pasture natural regrowth in the Northwestern amazon. Numbers were assigned to the morphospecies based on their maximum taxonomic resolution, with "L" used for larval stage morphotypes and "N" for nymphal stage morphotypes. Density in individuals/m2; Mass in alcohol in mg/m2.

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Supplementary material 3

Pearson correlation coefficient

Authors: Daniel Castro, Clara P. Peña-Venegas, Carlos H. Rodríguez-León, Ervin H. Duran-Bautista, Armando Sterling

Data type: docx

Explanation note: Pearson correlation coefficient describing the relationship between density, biomass, richness, functional groups, main soil macroarthropod taxa groups and main soil physicochemical properties with the two first principal components. Significant correlation is indicated: * = $p < 0.01$; ** = $p < 0.001$; *** = $p < 0.0001$.

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